Where Are Your Fingers?

Lindsey Ellen Fraser

A DISSERTATION SUBMITTED TO

THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Graduate Program in

Psychology

York University

Toronto, Ontario

November 2019

Abstract

How do we know how our fingers are oriented in space? Contributions to limb and finger perception include afferent sensory signals from the muscles, joints, skin, as well as vision and other senses, and top-down assumptions about the body's dimensions. A growing body of literature has examined the perception of finger and hand position and dimensions in a bid to understand how the limbs are represented in the brain. However, no studies have examined perception of the orientation of the fingers. A comprehensive model of highly articulated body parts must include perception of their orientation as well as their position. This dissertation seeks to fill an existing gap in the literature by exploring contributions to finger orientation perception, using a novel line-matching task. In Chapter 3 I provide evidence that vestibular disruption using galvanic vestibular stimulation (GVS) leads to an inward rotation of perceived finger orientation, and provide some evidence that finger orientation perception may not be accurate at baseline. In Chapter 4 I show that left- and right-handers may have different strategies for finger orientation perception, and provide evidence for an outward rotational bias that increases as the hands are placed further laterally from the body midline. In Chapter 5, I show that the way the probe line is initially displayed has a significant impact on performance, specifically on asymmetries of responses for the two hands and the compression of responses across the test range. I further show that the outward bias observed in Chapter 4 might be due to order of hand placement and differences in muscle strain across conditions. In Chapters 6 and 7, I show no difference in orientation perception for the ring and index fingers, but find an overall inward rotation of orientation estimates for palm-down hand postures, compared to palm-up postures. My research clearly shows that perceived finger orientation, as measured in my line-matching paradigm, is highly context-dependent. I discuss this in the greater context of the limb perception literature and outline some of the questions which much still be addressed in order to arrive at a comprehensive model of hand and finger perception.

Acknowledgments

I want to thank Dr. Laurence Harris, who has been my mentor, adviser and friend for the last seven years. It's hard to believe a conversation about bats at a CVR summer school turned into all of this. Laurence has given me so many opportunities to explore my own ideas, connect with researchers from around the world at conferences and events, and pursue side projects which have helped me develop into the scientist I am. Throughout these seven years he has been an unfailing support in my struggles, and the biggest cheerleader in my successes. Thank you, Laurence, for this great experience and for always holding open the door for your students to learn and grow.

To my committee members, Dr. Rob Allison and Dr. Denise Henriques, thank you for your guidance and feedback through the years. A special thank you to Denise, the current director of the IRTG program, who has worked tirelessly to give use trainees as many opportunities to succeed as possible.

To the members of my lab, past and present: Meaghan, John, Nils, Sarah, Yasmeenah, Bob and Stefania, you guys are the best lab I could ask for. Thank you for all your advice, encouragement and support, in science and in life. You guys are absolutely crazy for agreeing to all of my ridiculous adventures, and it's fantastic. Having enthusiastic, silly, dedicated, devastatingly smart colleagues has made this PhD a ride. Cheers.

To my extended CVR family, Cyan, Marcus, Maria, Shanaa, Devin, George, Khushbu, Adam, Bianca, Naail, Lily, Janis, Tom, Parisa, Lina and all the others with whom I've shared drinks, frustrations, celebrations, movie nights and more: I'm incredibly lucky to have such a great people to take this journey with. Sometimes grad school is commiserating over beers on a Thursday, sometimes it's running for your colleagues the night before an abstract deadline, or crowdsourcing stats help. And sometimes its hiking in the German Alps, whitewater kayaking, and cooking steaks over a campfire in the backcountry of Algonquin Park. It's the people that make this experience what it is. Thanks for being such an amazing crew.

A massive thank you to all of the admin and staff who have kept the Psychology Grad Office and the Good Ship CVR afloat: Teresa, Irit, Lori, Freda, Adrienne, and the effervescent Barb. Your support is what lets us grad students flourish.

Thank you as well to NSERC, and OGS, and the CREATE and VISTA scholarships that have helped me focus on science, and have given me so many opportunities to go beyond the curriculum and become a well-rounded researcher.

Thank you to Ms. Wood, the high school science teacher who told me to never stop asking questions. I'd say I took your advice and ran with it.

Finally, thank you to the two people who have been my biggest champions my whole life. Lynn and Don Fraser, I promise I won't make you read this entire monster document. Just know that it represents a love of knowledge and ideas, and five years of hard work, that are modelled after the passion and work ethic with which you both approach life. Thank you for all your encouragement and for only slightly panicking when I started travelling to conferences all over the world. You've always been in my corner and I am endlessly grateful.

Contents

List of Tables

List of Figures

1 Introduction

Our hands are our most dextrous, and arguably most useful, tools for interacting with the world. One need only turn out the lights and try to navigate through a room to realize just how valuable our hands can be, not only as effectors but also as sensors that can tell us about the world. Yet in order to use haptic information, we must be able to interpret sensory feedback stemming from the hands in the broader context of our bodies and our environment. If, while stumbling in the dark, my hands were to fall upon an animal's paw, an understanding of the size of my hands and their position relative to one another is vital for deciding whether I have encountered a little cat or a large tiger.

This dissertation explores how we keep track of our hands and fingers in space. What sensory information is relevant? How does the experimental task influence performance? How do characteristics like handedness, hand posture, and hand location affect our ability to report how our fingers are oriented? A comprehensive model of body perception must include an understanding of how the hands and fingers are mapped in space. This knowledge not only informs the study of those with neurological impairments related to body perception, but can also inform the design of prosthetics, tools, and virtual body applications.

Contributions to limb position perception

Proprioception, or kinesthesia, is the sense of our body's position and movement in space. Although body perception is inherently multisensory, proprioception refers to a subset of sensory inputs from receptors in our muscles, joints and skin, which tell us about the movement and posture of the body [140, 141]. Other senses such as vision and touch can supplement, or potentially override, these inputs when forming the final estimate of our limbs' position in space. In this section I will provide a short overview of what is known about the contribution of each of these inputs to limb localization, with an emphasis on the consequences of disrupting or removing these inputs.

Muscles. Receptors in the muscles, known as muscle spindles, monitor the shear forces of a muscle during lengthening, shortening, and contraction [119]. These signals help determine the position of the limb [141]. Applying vibration to a muscle elicits spindle activity and creates the sensation of the muscle being extended or lengthened [90]. This reliably leads to displacement of perceived limb position [25], sometimes even beyond the range of possible movement [26]. Illusory displacement of the hand has also been found with electrical stimulation of the muscle [48]. Muscle conditioning can also influence perceived limb position: working with anesthetized cats, Gregory and colleagues showed that tensing and relaxing elbow flexors without changing their length, can lead to subsequent changes in the background activation of associated muscle spindles. In humans, this tensing and relaxing leads to displacements of around 5° in perceived arm position [63, 64]. Due to the thixotropic properties of the muscles, this conditioning is effective for short and medium muscle lengths, and primarily in passive movements [141, 142]. Muscle loads and perturbations can also partially impair limb perception. Rymer and D'Almeida examined finger joint position sense using a position matching task, while applying various loads to the joint; joint position was accurately reproduced for free movement and while supporting a muscle load, but when participants were instructed to actively resist the load imposing the joint movement, they made significant position matching errors in the direction of the applied force [150]. Finally, muscle fatigue following repeated movement or exercise can cause the position of the arm to drift [15] and increases position matching errors in the direction of flexion [2, 176]. Given that muscle receptor activity is highly dependent on past states, it had been argued that it is not an ideal indicator of position sense [139]. Nevertheless the evidence strongly suggests that muscle spindle activity contributes substantially to position sense.

Joints. There is evidence that the sensory nerve endings in the capsules around the joints contribute to position sense. Clark and colleagues found that anesthetizing the knee joint led to contralateral position matching errors of around 1.9°, although they did not find any errors in another condition where both the joint and the skin around it were anesthetized [19]. Ferrell and Smith used a digital nerve block on the hand and found finger position sense was not impaired for finger bends well within the range of motion, but lead to position matching errors at extreme positions. This led the authors to postulate that joint receptors are useful as “limit detectors” and play a more important role at the boundaries of the range of motion [42, 43]. Clark and colleagues used local anesthetic to block joint receptors in the ankle, and in the metacarpophalangeal joint of the finger. They found impaired joint movement sense following these procedures, suggesting joint receptors also contribute to self-motion perception [18].

Skin stretch receptors. Cutaneous stretch receptors also inform position sense. Artificially stretching the skin around joints (e.g., using athletic tape) leads to illusions of the joint being more bent than actual; this has been shown for finger, knee, and elbow joints [23–25, 35]. Collins and colleagues varied the degree of stretch at the elbow and found increased position errors for stronger cutaneous stretching, suggesting a certain degree of sensitivity [25]. Some authors have postulated that skin stretch receptors may be particularly useful for disambiguating muscle spindle activity for muscles that control body parts in a different body segment (e.g., the fingers, which are controlled by muscles in the palm and forearm) [24, 35].

Motor commands. Gandevia and colleagues [49] examined the role of motor command signal in estimations of arm position by paralyzing and anesthetizing participants' right arms and asking them to attempt to move their arms and indicate their position. In the absence of actual movement, the motor command alone induced deviations of perceived arm position in the direction of intended movement [49]. The results are consistent with studies showing that the phantom limb of amputees or deafferented patients can move as a result of motor commands [47, 145]. When participants simply will their restrained finger to move, this produces localization errors that scale with effort [163]. Thus, there is compelling evidence for an influence of motor commands and expected movement outcomes in final estimates of limb position.

Vision. The contributions of visual input to position sense merit a much larger discussion than the one here. As my dissertation focuses on position sense in the absence of vision, I will restrict this section to a brief overview of the role of vision in the calibration of position sense. The visual system provides absolute measures of length and width that can help calibrate proprioceptive signals, which communicate position vectors but not dimensions (see below). Electrophysiological work by Graziano suggests that visual and proprioceptive limb position sense is integrated as early as primate premotor cortex [62]. A key principle of sensory integration is that more reliable senses are weighted more heavily when combining multiple individual sensory inputs into a single position estimate [37–39]. A consequence of this weighting strategy is that precise, visually-informed position sense can easily dominate noisier proprioceptively-informed position sense. Simply observing a false limb for a while can lead to a drift of proprioceptively-perceived limb location in the direction of the false limb [149]. When participants adapt to a visuomotor transformation in space, proprioceptively-guided position sense quickly recalibrates [27] and this recalibration persists across several absolute positions in space [52]. Visual feedback about limb position can guide, refine and recalibrate proprioceptive position estimates; however, this means that vision can also easily ”capture” or bias final position estimates, leading to potentially erroneous recalibration of proprioceptive inputs.

Somatosensation. Tactile information provides cues to the position of body parts relative to objects in the world (e.g., the feeling of my arm resting on a table) or relative to each other (e.g., my thumb pressing against my fingertip). A moving pattern of tactile information can also be used to cue an individual to self-motion [70]. While tactile cues such as pressure or contact with surfaces can provide information about body and limb position, localization of discrete tactile events is influenced by dynamic body position [4, 5], and gaze [69, 138], suggesting that body position is used in the coding of tactile events [120]. It has been proposed that proprioceptively-sensed body position is used to help align tactile and visual maps into a single reference frame [11]. The interaction between proprioception and somatosensation is clearly both complex and bidirectional in nature.

Graviception. Determining the absolute positional estimate of the limbs, particularly in the absence of vision, requires knowledge of how the body is oriented in space. Vestibular signals provide a measure of the head’s orientation relative to gravity, and “somatograviceptors” in the gut provide information about the orientation of the trunk [127, 128]. These inputs, along with vision and somatosensory pressure cues, can be used to form an internal estimate of the body’s orientation in space [6, 34], which can then aid in transforming egocentric position estimates into absolute spatial coordinates [107]. The vestibular system has also been implicated in cortical networks that contribute to sensory integration [168]. Artificial activation of the vestibular system by galvanic vestibular stimulation (GVS) can improve body position sense in those with neglect [158]. In healthy adults, GVS creates errors in arm positioning during movement [13, 115]. Knox and colleagues reported that participants showed errors in replicating arm positions encoded while experiencing GVS [88]. A related method of vestibular stimulation, caloric vestibular stimulation (CVS), can modify the perceived location of touch on the hand [40], leading some authors to suggest that the vestibular system is critical in forming and maintaining an underlying map of the body in space [109]. In Chapter 3, I will focus on the influence of vestibular disruption on the ability to track passive finger movements, and to maintain a sense of the finger's orientation in space. For more details on vestibular influences on position sense, please see the Introduction of Chapter 3.

Non-sensory contributions. In addition to bottom-up sensory inputs, a number of top-down influences can impact perceived body position. Ghilardi and colleagues report a study in which they measured deviations of perceived hand position and found errors in the direction of what they refer to as a "common operating location," that is, a default manual workspace directly in front of the body. They further showed that training participants to work in a novel workspace led to subsequent drifts of hand localization towards the new workspace, suggesting a tendency of limb position sense estimates to drift towards probable or learned locations [52]. While unintentional muscle conditioning must be considered as a possible confound, these data nevertheless suggest that past experience and training can influence limb position sense.

Context, training, adaptation, and *a priori* assumptions about the body can influence final limb position sense. In particular, the proprioceptive sense alone requires some internal map of the dimensions of the body in order to be resolved into a final position estimate. This internal body map is the focus of the section below.

Proprioception and internal body maps

Sensory signals from the joints, muscles and skin do not provide any information about the absolute length of limb segments. In order to determine the absolute position of body parts, the brain must have some internal sense of these dimensions, i.e., an internal body map. It has been suggested that afferent proprioceptive information about the body is consolidated with this map to determine the absolute spatial location of the body and limbs. [141].

The notion of an internal map of the body's dimensions was first introduced by Head and Holmes [71]. Internal body maps are not only relevant for determining our own position and posture, but for interpreting sensory inputs caused by external sources. When we infer the height of a branch by how it brushes our shoulder, or the size of a ball based on how much space it takes up in our palm, we are using an internal sense of our body's dimensions to decode sensory inputs into features in the world. Some scholars have suggested that our internal sense of the length of body parts, specifically the hands, may act as a yardstick for gauging the length of objects in the world [95].

Some of the strongest evidence for an *a priori* map of the body in the brain is the condition of phantom limb syndrome. Following amputation, some individuals experience a sensation of the body part's continued presence, i.e., a "phantom," a sensation which may persist for years following amputation [14, 130, 131]. Phantom body parts can also be invoked by anesthesia [125], though they are immediately abolished when visual feedback of the real limb is provided. Such lingering percepts could not exist without some kind of persistent representation of the body in the brain.

Internal representations of the body have been referred to by many names, including *body matrix*, *body schema*, *body image*, and *body model*. The proliferation of terms in the literature reflects a general disagreement about the exact number of body representations employed by the brain and under what circumstances these representations are recruited [77]. Here a clarification must be made: I have referred to the *a priori* collection of knowledge about the dimensions of the body as a body map, which describes a low-level set of estimates of length and width of individual body parts. Body representation, by contrast, often describes higher-order integrations of body map(s) with real time proprioceptive information and other *a priori* assumptions (regarding, for example, plausible range of motion, volumetric properties or visual features of body parts).

Although a full literature review of the debate on body representations is beyond the scope of this dissertation, it should be noted that there is general agreement that there are separate body representations for *action* and for *perception* (usually, but not always, referred to as the body schema and the body image, respectively). This distinction was first noted by Head and Holmes [71] and has been echoed by others [28, 133, 160]. Martel and colleagues concisely describe the body schema as “a highly plastic representation of the body parts, in terms of posture, shape, and size, that can be used to execute or imagine executing movements accurately” [116, 123]. The body image, what Di Vita and colleagues have more precisely called “non-action oriented body representation” is “a pictorial description of the body mainly based on visual exteroception” [30]. The body image has been further proposed to be comprised of two distinct components, a visuospatial map detailing the structural relations of body parts, and a semantic or conceptual understanding of the body’s components [16, 160, 162].

Neural pathways of high-level body representation

A number of clinical studies have reported double dissociations between the ability to recognize or point to body parts (impaired in conditions like autopagnosia) and the ability to use those body parts to complete tasks (impaired in conditions like apraxia) [76, 133]. These dissociations suggest distinct pathways of body representation for action and perception. A similar division in pathways can be found in vision [61], touch [10], and audition [98]. Just as initial what–how visual pathways have been found to interact, the total independence of body representations for action and perception has also been questioned. De Vignemont adopts a Bayesian framework and conceptualizes the difference between the two kinds of body representations as a difference in the relative weighting of online and *a priori* information about the body [28]. Within this framework, representations for action emphasize dynamic information required to execute movements, whereas representations for perception emphasize stored knowledge about the body and its features [28].

A clinical study of 70 stroke patients showed that lesions in left temporal areas of the brain selectively impaired perceptual and semantic representations of the body, while damage to dorsolateral frontal areas and parietal areas affected body representations for action [160]. This is consistent with other evidence suggesting that temporoparietal lesions can impair higher-order forms of conscious body perception, such as perceived ownership [168]. Meanwhile, imaging studies have identified the posterior parietal cortex (PPC) as being involved in integrating visual information about targets with proprioceptive coding of reaching and motor control, implicating it in perception of the body for action [21, 84]. Tsakiris has suggested that the network of body representation in the brain begins with online representations of the body in secondary somatosensory cortex. Integration of this representation with proprioceptive signals relevant for action then occurs in PPC, while conscious processes related to self-recognition and self-concept occur in insular cortex [31, 166]. This theory fails to account for neuroimaging and neuphysiological data implicating the activation of premotor and primary motor cortices in representations of the body for action [30, 62, 134], suggesting a more comprehensive understanding of body representation networks is still needed.

Multisensory basis of body representations

If the primary role of internal body maps were to be to provide a framework for understanding the spatial relations between proprioceptive, somatosensory, and visual information about the body, then it should not be surprising that the areas associated with body representations are also areas implicated in multisensory integration. It has been argued that body representations themselves are derived from cross-sensory contingencies that occur over time [28], and this is the foundation for the sense of body ownership [166]. The observed dimensions of body parts, identified via repeated cross-sensory contingencies, may help construct an abstracted model of the body's dimensions and properties—the basis for the internal body map. This map can then be used to calibrate and interpret dynamic visual, tactile, and proprioceptive information [166].

Since cross-sensory contingencies are recognized by infants less than a year old [183], it seems likely that body representations are formed early on in development. In adults, however, it is knowns that body maps are highly plastic: manipulations of visual feedback about the body's dimensions can quickly update internal assumptions about limb length and size [85, 96]. At the same time, the internal body map may fail to update properly following observable changes in the body, as is the case with phantom limbs [14]. The flexibility, context-dependence and adaptive properties of internal body representations form a fascinating and active area of research. In particular, developments in avatar embodiment in virtual reality have opened up new venues for testing the flexibility and limitations of internal body representations [110].

Curiously, tactile localization of stimuli on the hands is distorted by caloric vestibular stimulation [40], and perceived landmarks of the hand are also mislocalized [109]. Some authors have posited that the internal body map can be directly influenced by vestibular disruption [109], while others suggest that added vestibular noise may result in a stronger reliance on a non-veridical, *a priori* body map [53]. The contributions of the vestibular system to internal body representations is a fascinating topic which deserves more attention in the literature.

A default body position?

In Head and Holmes' original description of the body schema, they include a default posture, to which other transient postures are compared before entering consciousness [71]. Since that original publication, considerable evidence has emerged to support a relatively static, internal map of the body's components, dimensions, and appearance. Though this map is not immune to external influences like sensory recalibration and adaptation, its existence is nevertheless widely accepted. Yet, the nature of a default or canonical body *position* is still not well understood.

Two lines of experimental research have emerged to support the possibility of a default positioning of internal body maps. The first is based on the crossed-limbs paradigm, where participants must make order and position judgments for tactile stimuli delivered to the left and right arms. Crossing the arms in space consistently leads to misreporting of temporal order for these stimuli [161, 181]. Crossing the feet, or crossing a hand and foot, leads to similar impairments in temporal order judgments [155]. Localization of tactile stimuli on the hands also becomes confused when the hands are crossed [4], although this confusion resolves with practice [5]. Some authors have suggested that crossed-limbs effects reflect a rapid re-encoding of tactile stimuli into external spatial coordinates [155], which requires an interim step of determining the position of the limbs in space. Data from crossed-hands studies suggest that the spatial location of the left and right hands might be inclined towards a default position which cannot be corrected for in time to make rapid judgments. The complexity of the task is important: Shore and colleagues note that for temporal order judgments, the effect is specific to bimanual crossed-limb judgments, while single tactile events are remapped accurately [161]. Thus there is some evidence for a default positioning of body parts, which must be disentangled when making rapid comparisons of touches felt across the body.

The second line of research supporting default body positions is that of limb ownership. Perceived ownership over a false limb, induced by the Rubber Hand Illusion (see [12]), is constrained by the viewed position of the false limb. False limbs which are positioned in incongruent orientations, such as rotated 90° from the first person perspective, do not elicit ownership illusions as strongly as hands positioned in such a way that could conceivably be a part of the body [135, 169] (though they may still invoke some proprioceptive drift; see [72]). False limbs which do not resemble a human hand also do not elicit the illusion as strongly [167, 169]. It has been argued that visual and positional information contained in internal body maps acts as a criterion for what individuals are willing to consider a part of themselves [166, 169]. The first-person perspective also provides an advantage in temporal delay detection in finger movements [73], suggesting felt limb ownership can convey other measurable perceptual advantages. These findings raise an interesting possible application for ownership illusions and body ownership as a probe for the default position of internal body maps. By varying the position and orientation of false limbs and measuring subsequent strength of body ownership illusions, it may be possible to plot a probability distribution for the position of the ”canonical” body. To my knowledge this work has not yet been done, although a study by Cadieux and colleagues suggests that the rubber hand illusion does not work for false limbs that cross the body midline [17], consistent with crossed-limbs research suggesting this configuration is incongruent with the internal body map.

How a single default body position, or several default body positions, might develop is an open research question. One possible candidate is based on comfort: Bromage and Melzack have proposed an “orthopaedic” resting state in which the muscles of the body are the least flexed or extended. This position is the same one in which phantom limbs tend to appear [14], and which astronauts in microgravity may tend towards [69]. Alternatively, work by Ghilardi and colleagues on perceived hand drift toward learned manual workspaces, suggests that the default body position may be a product of experience over time— that is, the default body position is based on the common functional poses we adopt in everyday life [52].

Mapping the hands in space

The hands and fingers occupy a disproportionately large area of somatosensory and motor cortex compared to other body parts [136]; they also pose a particular challenge for body representation. Being highly articulated, with many joints and skin folds, as well as being controlled predominantly by muscles in the arms, means that resolving dynamic proprioceptive signals about the position and posture of the hands and fingers is computationally intensive [141, 159]. Converting these signals into absolute spatial positions requires a knowledge of the dimensions of individual segments of the hand, between each of the joints, as well as the length of the palm and both sections of the arm. Internal representations of the hand, at least for action, must also be flexible enough to incorporate sudden changes in the effective size and shape of the hand brought about by clothing like gloves or mitts.

When visual feedback about the fingers and hands is available, their absolute position can be coded in visuospatial coordinates and compared against afferent proprioceptive inputs. This mapping can be to direct motor adjustments required for precision movement, confirm hand ownership, or any number of other tasks. Computing absolute hand and finger position from proprioceptive signals and internal body maps alone, however, is less precise and prone to error over time. In the next section I will discuss some methods of measuring the accuracy of non-visual localization of upper limb position, and some of the findings of these methods.

Measuring hand and arm localization

One of the easiest methods for probing the perceived position of body parts is to ask participants to point to them. This method, described by Head and Holmes in 1911 [71], has been implemented in a number of studies on both clinical and healthy populations. In 2010, Longo and Haggard described a task in which the participant's left hand was masked, and the participant pointed to the tips of the fingers and the knuckles using a pointer [103]. This approach consistently results in participants overestimating the width of the hand (judging the knuckles and fingers to be spaced further apart), and underestimating the length of the fingers, on a gradient with the largest underestimation occurring for the pinky and ring fingers, and the least underestimation for the thumb [99, 100, 102–104, 106, 121]. This distortion is found for the back of the hand; similar but reduced errors are seen for the palmar surface of the hand [104].

The method of pointing to body parts as a measure of the fidelity of internal body representations has been criticized for ignoring the possibility that the pointing hand contributes its own source of error [28]. To illustrate this, imagine a scenario in which a person must touch their right index fingertip to their hidden, left index fingertip. If there were indeed a difference in the final location of the two fingertips, might that error stem from 1) an error where one thinks the left finger is, 2) a mismatch of where the right finger is pointing versus where it is intended to point, or 3) both? As De Vignemont has highlighted, body landmark pointing tasks do not examine the accuracy of pointing to other predetermined, unseen locations in space as a control condition. So the percentage of error that can be attributed to a distortion in the underlying representation of the goal body part, and the percentage that may be caused by errors related to the pointing task, remains unclear [28].

In a pointing task, a difference signal between the perceived position of the goal body part and the pointing body part must be computed, and then reduced. In this way, pointing tasks are similar to joint position reproduction (JPR), where the posture of the limb must be either remembered and reproduced (ipsilateral JPR) or reproduced by the contralateral limb (contralateral JPR) [68]. Here, the signal being computed is the difference between the joint angles of the two limbs, or between the limb and a remembered posture [59, 67, 141, 170]. There is some evidence for a handedness advantage in JPR tasks. In a series of studies Goble and colleagues showed that right-handed participants have a nondominant arm advantage for both contralateral and ipsilateral JPR [55–58, 60], and report that left-handed individuals show the same nondominant arm advantage [60]. However, other labs have reported no difference between the two arms in other forms of JPR tasks [87].

Sainburg's dynamic-dominance theory of handedness purports that the dominant limb is specialized for precision control and manipulation, while the nondominant limb is specialized for force control and stabilization [143, 151, 152]. This is especially evident in bimanual tasks such as chopping or writing, where the nondominant limb holds an object while the dominant limb interacts with it. JPR data suggesting that the nondominant limb is more efficient in replicating joint angles (useful for force control) support this theory. When right-handers instead move their arm to match the endpoint position of a visually presented target, there is a dominant arm advantage, consistent with specialization of the dominant limb for endpoint localization [57].

As with pointing localization tasks, JPR and active matching tasks often do not consider the matching limb's contribution to position errors. This is especially concerning given that there is evidence for asymmetries in joint angle and endpoint matching between the dominant and nondominant limbs. Adamo and Martin directly investigated contralateral JPR using the right or left arm, and found limb-specific positioning errors distinct from ispilateral JPR, which was more accurate [1]. These results suggest that contralateral joint matching may introduce cross-limb errors that do not reflect the perceived position of the target limb. Pointing and matching tasks tell us something interesting about the ability to judge the relative positions and postures of body parts. However, errors in these tasks cannot be conclusively ascribed to errors in the perceived position and location of the target body part.

Other measures of body representations include template-matching tasks, where participants identify correct images of their body from distorted alternatives [103] and line length estimation tasks where participants adjust a line to match the length of a body part [97]. For the hands, at least, there is evidence that template matching can be done accurately [103] although line length tasks show an underestimation of finger length similar to the errors observed in pointing tasks [105]. That is, tasks probing individual characteristics of a body part like length and width may be more prone to error than tasks accessing global characteristics like shape and outline.

Another method of measuring spatial body representations is to ask participants to report the location of the unseen hand or body part with respect to a visually cued location in space. In this task, the primary goal is to determine the absolute spatial coordinates of the body part, convert this location into to visual coordinates, and compare it to the position of a visual probe. The task resembles the initial stages of goal-directed movements in that target and proprioceptive spatial coordinates must be compared within the same frame of reference. At the same time, the task requires consciously accessing this comparison in order to respond. If we were to adopt the framework that the integration process for body representations for action and perception is the same, but with varying weightings of contributing parameters, then this task would arguably fall somewhere between pure representation for action (coding goal and effector positions) and for perception (visually representing perceived body location). Therefore, this type of task may be uniquely poised to address characteristics relevant to both kinds of body representation. Furthermore, passively positioning or moving the hand eliminates the contribution of motor efference copy to position estimates [124], thus emphasizing afferent proprioceptive and internal body map information.

Schmidt and colleagues tested perceived hand position by slowly rotating participants' arms about the elbow in the horizontal plane and asking participants to report when their index finger passed under a visual LED target. They reported that perceived finger location was rotationally biased inwards towards the body midline in right-handers, for both younger and older adults [156, 157]. Qureshi and colleagues measured the perceived location of the right fingertip by placing it in a position with respect to the body midline, and asking participants to indicate which line on a ruler best corresponded to its perceived position. They too found perceived position was biased towards the body midline, and this bias increased as the actual distance of the finger from the midline increased [144].

In both of these tasks the finger is used as a probe for the position or orientation of the hand and the arm, and minimizes the number of joint angles between them. However, an outstanding question is whether the orientation of the finger is something which can be judged on its own. In everyday life the fingers take on a variety of positions that may not be parallel with the hand or arm. Can we accurately report the orientation of our own fingers, and what cues influence this representation?

This dissertation

This dissertation explores the accuracy and precision of index finger orientation perception, as an assay of how well distal portions of the limbs are spatially localized. In particular, I am interested in the factors which influence accuracy and precision of perceived orientation of the fingers, as these same factors likely contribute to the formation of internal body maps, proprioceptive sensing, or the integration of the two. This research is intended to complement the existing literature on hand and arm localization using visual mapping techniques in the hope of arriving at a more comprehensive model of dynamic body perception.

Chapter 2 outlines the general methods implemented in all experiments, including the apparatus and testing paradigm used. To summarize, participants' hands were obscured from view, and they had their index finger passively rotated about the proximal interphalangeal joint. They then rotated a white line presented on a screen imposed over their hand, until it matched the orientation of their finger. In this chapter I will also outline conventions for analyzing and presenting data, including the coding of directional errors as inwards/outwards to compare anatomically similar positions for both hands. Further methodological details specific to each experiment are described in subsequent chapters.

Chapter 3 explores the contributions of vestibular signals to finger orientation perception. Disruption of normal vestibular functioning may lead to errors in hand and arm perception. In a suite of four experiments, I compare perceived finger orientation while participants experienced disruptive galvanic vestibular stimulation (dGVS), compared to when this stimulation was absent. I used a visual probe in the frontoparallel plane (Experiment 1), a non-visual probe (Experiment 2), and then repeated these experiments in the transverse plane (Experiments 3 and 4). Perceived finger orientation rotated inward under the influence of dGVS, for visual/proprioceptive matching tasks but not for non-visual/proprioceptive matching. In particular, perception of the left hand appears to be vulnerable to the effects of dGVS.

Chapter 4 examines the role of the location of the hand with respect to the body. Haptic judgments of spatial orientation have been shown to deviate outward as the distance of the hand from the body midline increases [80], suggesting that the orientation of the hand may be misjudged in more distal positions. Participants made orientations judgments of the left and right fingers while the hands were positioned in front of the body midline, in front of the ipsilateral shoulder, or twice the distance between these positions away from the midline. In addition, I looked at performance in both right- and left-handed participants. Perceived orientation of the fingers rotated outwards as the distance between the body midline and the hand increased. Left-handers were more variable in their responses, but on average were more accurate, compared to right-handers.

Chapter 5 assesses some of the methodological considerations of my task in more detail. In Experiment 1, I examine how the probability distribution of the visual probe's initial orientation during the response phase influenced performance. I include conditions where the probe's orientation was randomly sampled from several specified ranges, and a condition where the orientation was randomly sampled from a normal distribution about the correct orientation. Surprisingly, the conditions using random sampling from a range with equal likelihood produced asymmetries in errors between the left and right hands; by contrast responses to the probe taken from the normal distribution were 1) faster and 2) more accurate. In Experiment 2, I considered order effects in the placement of the hands with respect to the body midline. Participants completed the orientation judgment task with both hands in front of the midline first, or in front of the shoulder first, before completing the same task at the other hand position. When the hands were placed in the midline first, then positioned at the shoulder, orientation estimates in the second condition rotated outwards from estimates in the first condition. When the order of positions was reversed, no such difference was observed. This finding highlights how within-subjects designs may inadvertently introduce muscle conditioning that can influence responses in subsequent experimental blocks.

Chapter 6 compares finger orientation perception for the index and ring fingers. I tested orientation perception for the index finger for the left and right hands, as well as for the ring fingers, using an initial visual probe orientation drawn from a normal distribution about the correct response. While responses for the index finger were less variable compared to the ring, there were no observable differences between the accuracy of the two fingers. This result does not support previous assertions that the topography of the hand itself may be distorted in localization tasks.

Chapter 7 focusses on the role of hand posture on finger orientation perception. Drawing initial visual probe orientation from a normal distribution about the correct response, I assessed finger orientation perception for both left and right hands while they were pronated (palm down) or supinated (palm up). In consideration of potential order effects, this experiment was completed using a within-subjects design and a between-subjects design. Both analyses showed that when the palm was facing up, finger orientation estimates were biased inwards, towards the body midline, as compared to when the palm was facing down. These results underscore the lack of generalizability of orientation perception tasks across different manual contexts.

Finally, in Chapter 8, I summarize the findings of my research. How do we know where our fingers are? What factors influence our ability to judge the angle of our fingers in space? Our ability to accurately convert proprioceptive and body map information into visual coordinates depends on vestibular function, handedness, the nature of the visual probe, muscle conditioning, and hand posture. I then discuss these results within the context of the broader literature on limb localization and body perception.

2 General methods

2.1 Overview

All experiments in this dissertation use the same testing apparatus, and the same general procedure. Some participant characteristics and recruitment techniques are also common among studies. In addition, analysis was conducted using the same software and data cleaning procedures.

This chapter outlines the common methodological elements across studies in my dissertation. Deviations from this core methodology are mentioned in the relevant chapters.

2.2 Participants

All individuals who participated in this research were either undergraduate, graduate or staff members of York University at the time of data collection. Undergraduate student participants were recruited from the York University Undergraduate Research Participant Pool (URPP), and compensated for their time with credits towards their Introduction to Psychology course (0.5% grade credit per half hour of participation time). Graduate students and staff were recruited by word of mouth and were not given any compensation for their time. Unless otherwise noted, participants were all right-handed as indicated by self-report or by the Edinburgh Handedness Inventory (online edition, available at http://www.brainmapping.org/shared/Edinburgh.php). All participants reported normal or corrected-to-normal vision and had no pre-existing musculoskeletal or neurological disorders. All experiments reported in this dissertation were approved by the research ethics board at York University, and were run in accordance with the

Declaration of Helsinki (seventh revision, 2013).

2.3 Apparatus

A display monitor (ASUS VS247H-P 23.6” widescreen LCD) was mounted face-down on a metal frame, 44 cm above the surface of the test table. An integrated stepper motor (Applied Motion Products 23Q-3AE Integrated Stepper Motor, 20,000 steps/revolution) was positioned so that the motor shaft was either projecting towards the participant, 48cm above the table surface and approximately 45 cm in front of the participant’s cyclopean eye (configuration A) or projecting orthogonal to the table surface, 15cm above the table surface and approximately 35 cm from the participant’s midline (configuration B). The motor had a precision of 0.02°, emitted minimal noise while changing position, and gave no audible indication of direction of movement. The motor was programmed to accelerate/decelerate at a rate of 0.5 revolutions/s^2 to or from a preset velocity of 0.5 revolutions/s. A rectangular mirror was positioned either angled 45° in front of the participant (configuration A) or parallel with the screen and table surface (configuration B), so that the reflected screen images were optically superimposed at the depth of the motor shaft (see Figure 2.1). A soft foam block was provided as a cushion for the participant’s elbow; participants were free to move the cushion around to suit their comfort.

The motor shaft was fitted with a custom-machined metal clamp which held a small wooden dowel (8.5cm long; 0.8cm dia) such that the motor rotated the dowel about its central axis. During the experiment, the participant’s index finger was attached to the dowel with two lengths of flexible wire, such that their finger was held straight and rotated about the proximal interphalangeal joint. The rest of the hand and arm were unrestrained; a small foam block was provided for optional elbow support (see Figure 2.2).

The mirror obscured the participant’s hand from view. During the experiment, the lights in the room were turned off and participants were instructed to look at material presented in the mirror. They made responses using a standard computer mouse resting on the table under their free hand.

Testing equipment was controlled by a Macbook Pro using a VGA cable and one or

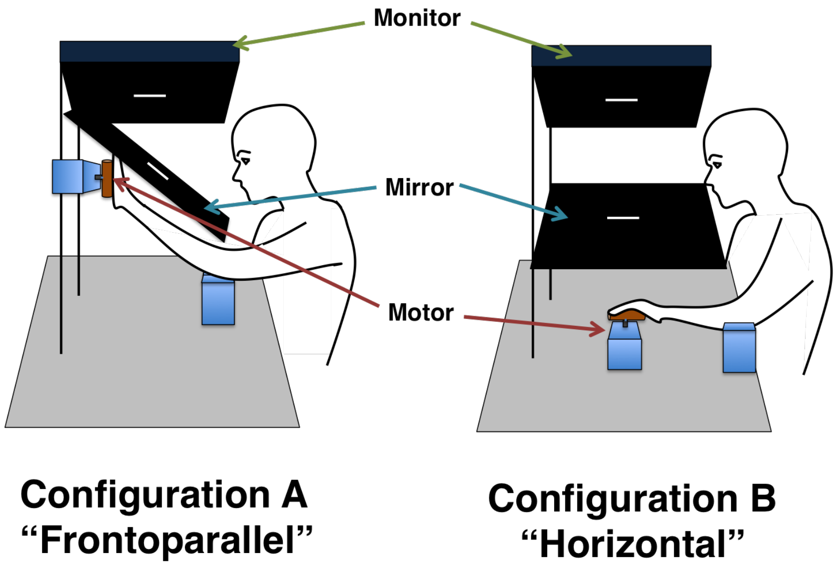

Figure 2.1: A schematic of the test apparatus in profile. In configuration A (left) the participant's hand rotated in the frontoparallel plane. In configuration B (right) their hand rotated in the horizontal plane. The mirror was arranged so that the visual line appeared at the same optic depth and location as the participant's obscured finger.

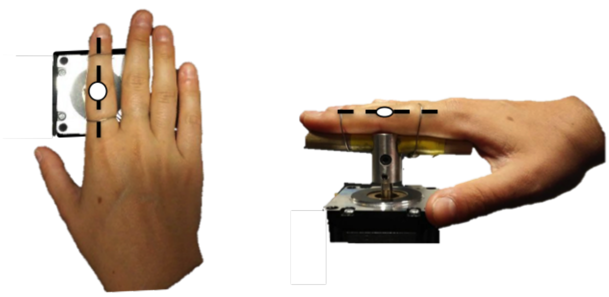

Figure 2.2: Two photos of the author's hand attached to the motor. During the experiment the motor rotated the participant's finger about the proximal interphalangeal joint (denoted by a white oval).

more RS232 USB to serial port adapters and a USB hub.

2.4 Software

I personally programmed all experiments in Matlab, either version 2012a or 2016b (MathWorks, Inc.), Experiments were implemented using the same program. Initial data processing, including calculation of mean response angles, was conducted in Matlab using the Circular Statistics Toolbox for Matlab by Philipp Berens [9]. Initial data cleaning was also conducted in Matlab. Statistical analysis was conducted using IBM's Statistical Package for the

Social Sciences (SPSS) (IBM, 2015).

2.5 Procedure

All experiments used the same core protocol described here. Procedural differences between experiments are discussed in the relevant sections.

At the start of a trial, a 250Hz beep sounded and the motor rotated the participant's finger to three initial "distractor" orientations, before coming to a stop at a fourth, "test" orientation. Test orientations were based on the specific experiment; distractor orientations were randomly drawn from a normal distribution using the normrnd.m Matlab command, with the mean of the normal distribution set as the final test orientation and the standard deviation set to 10° (this was intended to ensure that participants' hands moved to the test orientation from the left or the right with equal likelihood). Bounds were set such that the motor would not rotate beyond 40° in either direction, which might cause discomfort for the participant.

Once the participant's hand finger reached the test orientation, a second 250Hz beep sounded and an white bar (subtending 0.7° by 0.2° visual angle) appeared in the center of the screen. Participants could rotate this line (henceforth: "probe") about its central axis by clicking the left or right mouse buttons with their free hand. Participants were instructed to match the orientation of this line to the perceived orientation of their unseen finger "so that the line is parallel with, or overlaps with, your finger." Once the participant felt the probe was oriented correctly, they submitted their response by pressing the central scroll wheel button on the mouse. Submitting a response immediately started the next trial.[1]

Test orientations were repeated between 8 and 10 times, depending on the experiment. Trials were interleaved within a block, and the left and right hands were tested in separate blocks.

[1] Note that Experiments 2 and 4 in Chapter 3 use a variation on this response protocol. See the methods sections for those experiments for details.

2.6 Convention

Straight ahead and vertical are both coded as 0°. For the purposes of comparing anatomically similar positions of the hand, all other angles are coded as inward and outward deviations. A negative error would indicate a counterclockwise deviation of the left hand, and a clockwise deviation of the right hand. Similarly, a positive error would indicate a counterclockwise deviation of the right hand and a clockwise deviation of the left hand. See Figure 2.3 for illustration of this convention.

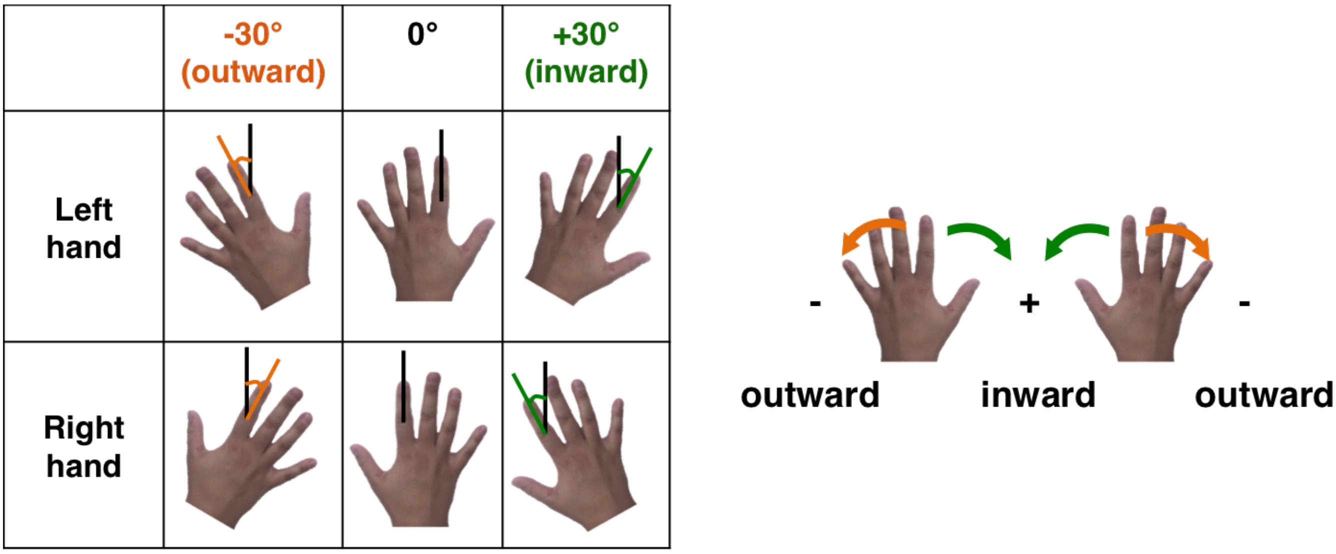

Figure 2.3: Illustration of the signing convention used throughout this dissertation. 0° indicates straight ahead/straight up. Negative values indicate an outward deviation, and positive values are an inward deviation. This is done in order to compare anatomically similar hand positions.

2.7 Data Cleaning

Participants were instructed to take their time and respond as accurately as possible. However, in a few cases, the participant indicated they made a response too soon or made a mistake in responding. In experiments described in chapters 5 through 7, these responses were recorded by an experimenter seated in the room and removed from the dataset prior to any data processing.

Remaining values were averaged across all responses for that test orientation, within a block. Average accuracy for a given test orientation was calculated by subtracting the test orientation from the mean response as calculated using circular statistics (e.g., a mean response of -16.5° for the test orientation -10° would result in a signed error of -6.5°). Average precision was calculated as the circular standard deviation of responses for a given test orientation within a block. Thus, participants had a mean accuracy and mean precision value for each of the tested orientations within a block.

All data were subject to an initial outlier removal prior to data analysis. Outlying values were identified as being greater than 2.5 standard deviations above the group mean for that test orientation for that specific block, or less than 2.5 standard deviations below the group mean. Given the interrelated nature of precision and accuracy, if either of these values was deemed an outlier, the value for the other measure was also removed.

For further details regarding data analysis, see methods sections for specific experiments.

3 Vestibular contributions to perceived finger orientation

3.1 Chapter Introduction

The vestibular system is crucially involved in body perception. The vestibular system provides an input to several multisensory areas in the brain that have been linked to high-level body perception, notably the right temporoparietal junction [166, 168]. Damage to these areas can extinguish a sense of body ownership, producing somatoparaphrenia, a disorder where body parts are misattributed to others, or ownership is assumed over another's limbs [171]. Galvanic vestibular stimulation (GVS), a method of electrically stimulating the vestibular organs, attenuates symptoms of these disorders [33, 89, 148] suggesting a (partial) recovery of normal body perception when the vestibular system is activated. A similar vestibular stimulation technique, caloric vestibular stimulation (CVS), has also been shown to invoke phantom limbs in amputees and paraplegic patients [3]. Giummarra et al. have interpreted these findings as suggesting that vestibular disruption may promote a more "standard" or prototypical representation of the body, i.e., a non-sensory, canonical percept of the physical self [54].

Vestibular stimulation modifies perception of the hands. Participants undergoing GVS become more susceptible to the rubber hand illusion, in which participants feel that a rubber hand is their own hand [108]. GVS also induces reaching errors [13], and disrupts maintenance of the hand's position relative to the trunk in complex movements [115]. These errors cannot readily be explained as mere compensations for an illusory sense of motion caused by GVS; rather GVS seems to interfere with the ability to track or represent the hand in space over time. CVS alters the perceived location of landmarks on the left hand, such that the hand is reported as larger than actual [109]. GVS does not seem to replicate this effect, although it shifts the perceived location of touches on the hand towards the wrist [41], suggesting that the perceptual representation of the hand may become exaggerated or distorted in the presence of erroneous vestibular information.

The role of the vestibular system in determining perceived hand orientation has not been investigated. Based on previous research showing the close connection between vestibular input and body representation, and vestibular disruption and body perception errors, I theorized that vestibular disruption might interfere with hand and finger orientation perception. This chapter details a set of four experiments looking at the effect of nondirectional, disruptive GVS (dGVS) on the perception of finger orientation in the frontoparallel and horizontal planes. In the general discussion I consolidate the findings of these four experiments, and discuss them in the context of literature on vestibular disruption, proprioceptive position sense and body perception.

Disruptive Galvanic Vestibular Stimulation *(dGVS)*

To disrupt normal vestibular processing, I used a galvanic vestibular stimulator (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada). The device was connected to a computer via a second serial port. A MATLAB program controlled the GVS output, the motor and the experiment display. Electrodes (1.25” dia, 9000 series, Empi Recovery Sciences, St. Paul, Minnesota, USA) were attached to the mastoid processes behind each ear and were secured with medical tape. A ground electrode was positioned on the forehead. In order to provide a disruptive signal to the vestibular system I used an alternating sum-of-sines voltage with dominant frequencies at 0.16, 0.33, 0.43 and 0.61 Hz (maximum current of 5ma, sampling rate 25ms). Time course of current for both electrodes is depicted in Figure 3.1. These parameters have been shown to elicit a sense of postural instability without a consistent sense of directional motion [112, 129]. Stimulation was bipolar, meaning that one electrode always emitted the inverse voltage of the other electrode.

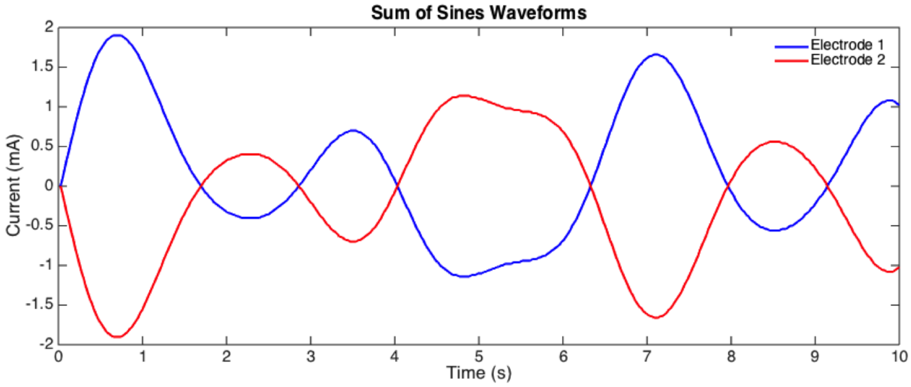

Figure 3.1: The sum-of-sines pattern of stimulation for electrodes 1 and 2, characterizing disruptive Galvanic Vestibular Stimulation (dGVS).

3.2 Experiment 1: Perceived finger orientation in the frontoparallel plane is affected by disruptive Galvanic Vestibular Stimulation applied before, during or after passive hand movement

3.2.1 Experiment 1 Introduction

In this study, I assessed participants' ability to report the position of their finger in the frontoparallel plane. I included three dGVS conditions, and one no-stimulation condition. In the dGVS conditions, dGVS was applied just prior to passive hand movement (”dGVS-Pre”), during passive hand movement (”dGVS-During”) or following movement, during the response phase (”dGVS-Post”). The rationale for these conditions was as follows: first, there is evidence that GVS may interfere with the ability to keep track of the hands' location in space while stimulation occurs [115]. If vestibular signal were to refine spatial location estimates of the hand, I would expect dGVS to produce the largest errors if it were applied while spatial location information is being encoded, i.e., while the hand is being moved (dGVS-During condition). However, there is evidence that landmarks on the hand are mislocalized even when the hand is held static [109], suggesting that vestibular inputs may contribute directly to some implicit representation of the body. If this were the case, then dGVS should produce the greatest errors when this representation is being accessed, i.e., during the response phase (dGVS-Post). The dGVS-Pre and control, no-stimulation conditions are both intended as control conditions for comparison purposes.

I did not control for potential aftereffects of dGVS after stimulation ended. There is some evidence for aftereffects of directional GVS, particularly biases in eye movements and verticality estimation in the direction opposite of biases experienced while stimulation is applied [111, 175]. The aftereffects of dGVS are not known. Additionally, previously reported aftereffects for directional GVS have been assessed following much longer periods of stimulation, from 5–20 minutes. It is not clear whether aftereffects would accumulate following repeated 4 second bursts of stimulation. I will return to the possibility of aftereffects of dGVS in the discussion section of the present experiment.

3.2.2 Methods

Participants

Thirteen participants (7 female, 6 male, aged 19-53) participated in this experiment. All participants identified themselves as right-handed.

Apparatus

The test apparatus was used in configuration A - "Frontoparallel" for this experiment (see Figure 2.1).

Procedure

Five test orientations were used in this study, ranging from -10° to 10° in 5° steps. Each test orientation was repeated 10 times in a block, resulting in 50 trials per block. Within-block trial order was randomly shuffled.

Four experimental blocks were administered in this study. In the Control condition, participants completed the task as outlined in General Methods: Procedure. In the dGVS-Pre condition, dGVS was triggered for 4 seconds, followed by a 3s delay before the motor began moving the participant's hand. In the dGVS-During condition, the stimulation was applied once the hand began moving, and ended when the hand came to a stop at the test orientation. In the dGVS-Post condition, the stimulation began once the hand had reached the test orientation and continued until the participant submitted their response. See Figure 3.2 for a visual depiction of the four conditions. Participants completed each of these four blocks for each hand, leading to 8 experimental blocks in total. Blocks were performed in a random order. Including instruction and set up, the experiment took roughly 1.5 hours to complete.

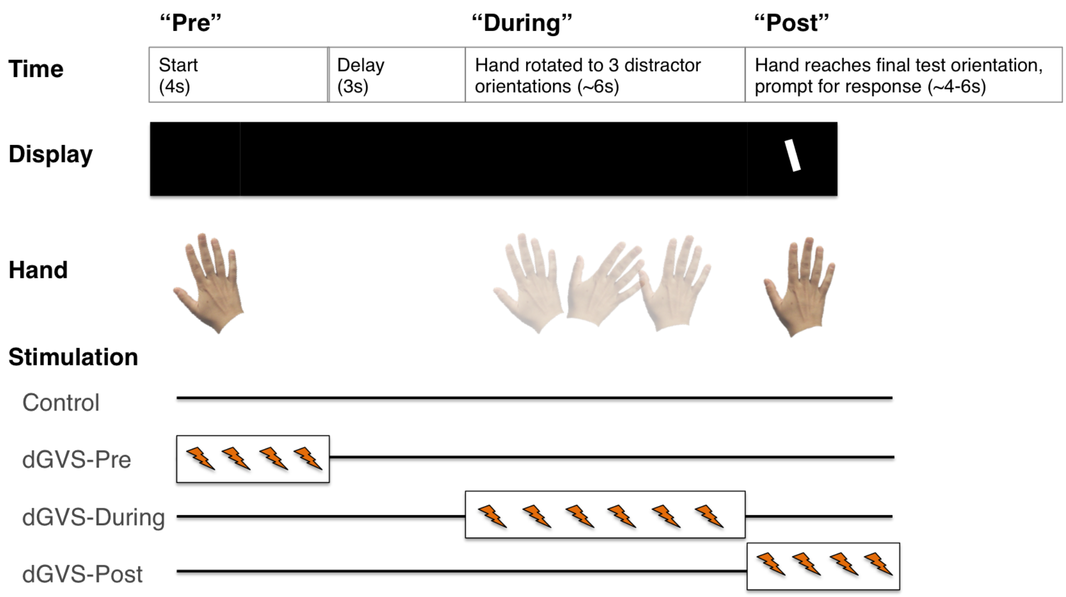

Figure 3.2: Time course of the four conditions in Experiment 1. Each condition was repeated for the left and right hands.

Data Analysis

Accuracy and precision values were calculated using the method outlined in Chapter 2.7. Initial outlier analysis led to the removal of 11 pairs of accuracy and precision values. Of 519 total pairs of valid values, 508 were used in the analysis.

Accuracy values were analyzed in a mixed model linear regression, with fixed effects of stimulation type (Control, dGVS-Pre, dGVS-During, and dGVS-Post), hand (left or right), and test orientation (-10°, -5°, 0°, 5°, 10°), and intercepts as a random effect. Degrees of freedom were corrected using the Sattherthwaite approximation [154]. A second analysis was performed on precision values using the same parameters. The mixed model regression was used instead of a traditional repeated measures ANOVA, because it allows for missing values without removing the participant's entire dataset from the analysis.

3.2.3 Results

Accuracy

Accuracy is the signed error (+ inwards/ - outwards) of the mean response of participants to a given angle. Mean accuracy for each of the conditions is shown in the top row of Figure 3.3.

The regression analysis found a significant main effect of stimulation type, $F(3, 456.04)=4.73$, $p=0.003$. There was also a main effect of hand, $F(1, 456.06)=49.67$, $p<0.001$, and a main effect of test orientation $F(4, 456.06)=53.08$, $p<0.001$. The stimulation type x hand interaction was also significant, $F(3, 456.04)=5.47$, $p<0.001$. No other effects were significant. Post-hoc contrasts, corrected for the hand-specific familywise false discovery rate using the Benjamini-Hochberg procedure [8], compared performance for each hand in each of the stimulation types. For the left hand, the three dGVS conditions resulted in performance significantly rotated inward from the control, $t(484.04)=-5.47$, $p<0.001$. For the right hand, there was no difference between the GVS conditions and control ($p=0.77$).

Taken together, these results indicate that the GVS conditions selectively impaired orientation perception in the left hand, by rotating responses inward relative to the left-hand control condition. Additionally, Figure 3.3 illustrates that at more extreme test orientations, participants' responses tended to err towards less extreme angles. This created a compression of responses towards finger orientations in the middle of the tested range.

Precision

Precision is the standard deviation of an individual participant's responses to a given angle. Mean precision for each of the conditions is shown in the top row of Figure 3.3.

The regression analysis found a significant main effect of hand on precision, $F(1, 456.04)=20.55$, $p<0.001$, and a main effect of test orientation $F(4, 456.02)=4.80$, $p=0.001$. No other effects were significant. That is, precision was worse for the left hand judgments compared to the right, and precision was worse at extreme test orientations.

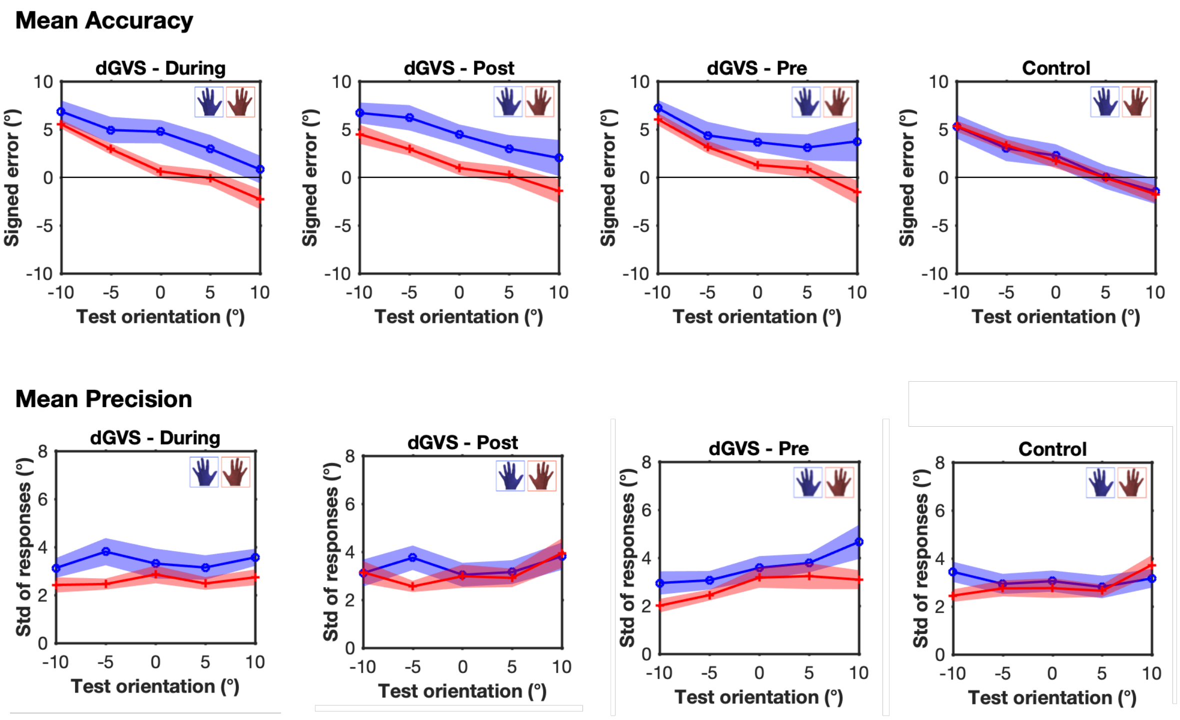

Figure 3.3: Top row: Mean signed error for each of the test orientations by stimulation type. Positive values indicate an inward rotation from vertical; negative values indicate an outward rotation. Bottom row: Mean precision for each of the test orientations by experiment. Shaded error bars are standard error of the mean.

3.2.4 Experiment 1 Discussion

In this experiment, I posited that dGVS would impair finger orientation judgments either as a result of 1) interference with maintaining a sense of the hand's spatial location (dGVS-During) and/or 2) impairing an implicit map of the hand accessed during response (dGVS-Post). To measure impairment, I looked at both deviations in participants' accuracy, as well as the variability in their responses across trials.

DGVS had an effect on all conditions in which it was present, including the dGVS-Pre condition. Specifically, dGVS produced an inward rotational deviation of left finger orientation estimates. Right finger orientation estimates were not affected. This task also produced a hand asymmetry in precision: participants were less precise with their left hand estimates compared to the right, regardless of the presence of stimulation.

I tested finger orientation with dGVS applied at different times, with the assumption that dGVS produced a discrete effect while stimulation was happening, and that carryover effects were likely to be minimal. While there is partial evidence for an aftereffect of *directional*

GVS on some measures of verticality perception and oculomotor responses where responses tilt in the opposite direction of GVS-induced sense of illusory tilt [137, 175], I had not anticipated that a nondirectional form of GVS like the sum-of-sines pattern would produce a directional aftereffect.

However, upon closer examination of the sum-of-sines signal in Figure 3.1, it is apparent that the approximately 4-6s of stimulation time used in this study, which always began from the start of the signal, may in fact have had a directional component. Specifically, the first 4s of the sum-of-sines waveform contained a largely positive current to Electrode 1 and a largely negative current to Electrode 2. This may have led to a subjective sense of leaning towards the cathode side during the experiment. While electrodes were consistently placed on the same side across participants, the location of the anode and cathode were not recorded; therefore I can only speculate as to what direction the illusory lean may have been.

Given this potentially directional stimulation, it is possible an aftereffect was present. Directional GVS has been shown to elicit aftereffects of nystagmus, and bias in verticality perception, directionally opposite to errors evoked during online stimulation [111, 175]. Individual variability in the length of the decay period for this aftereffect is high. MacDougall and colleagues report some instances of up to 6 minutes of reactive eye movements following 5 minutes of stimulation [111], while others report an exponential decay period following 20 minutes of stimulation, with a decay constant of 19.2 minutes [175]. These authors have highlighted the need for more research on directional and nondirectional GVS aftereffects, and particularly aftereffects caused by repeated stimulation. If the GVS stimulation applied in this study contained a consistent directional component, it is possible the aftereffects persisted for a long time. However if this were the case, we would observe different directions of errors for conditions where stimulation was occurring during response, vs. when it had already ended and aftereffects were present. Instead, the directional error is the same across all three conditions in this study. Thus my results don't support the possibility of an aftereffect of directional GVS driving orientation judgment errors. Instead, the consistency of the effects of dGVS across conditions suggests that these errors may be driven by a general sense of instability felt during and after the stimulation period.

I found selective effects of dGVS on finger orientation perception for the left hand in right-handed individuals. This finding is consistent with other research showing directional GVS selectively impairs left arm position in right-handed people [156]. Why would the left hand be more sensitive to effects of GVS? I submit two possible explanations: first, it could be that the representation of the dominant right hand is simply more robust against distortions (as evidenced by higher precision of estimates). Alternatively, it could be that the specialized role of the non-dominant hand as a position controller/force stabilizer [151,152] makes it more vulnerable to illusions related to perturbations of posture. That is, if the left hand were specialized for controlling position and stability of held or manipulated objects, then it stands to reason that it would be primed to respond to changes in posture or balance. As such, illusions of postural change may have a stronger influence on left hand position sense. These possibilities are not mutually exclusive, but require more empirical support. The next experiment in this study looks at the effects of prolonged dGVS on another, indirect measure of finger orientation perception: a comparison of finger orientation to gravity vertical.

Before closing this section, a final comment must be made on the effect of the outer test orientations on response. I found that the test orientations at the outer edges of the test range showed 1) greater variability in response and 2) errors towards the middle of the test range. Chapter 5 addresses some of the methodological problems that are likely the source of these effects. To summarize: the nature of the display line was such that it almost always appeared inwards of these test orientations, and the compression of responses likely reflects participants' stopping as soon as they reached a plausible response orientation. Please see Chapter 5 for more details.

3.3 Experiment 2: Perceived finger verticality with disruptive Galvanic Vestibular Stimulation

3.3.1 Experiment 2 Introduction

The line-matching task in Experiment 1 required matching a proprioceptive target (the finger) to a visual target (the line). A conversion must take place in order to make a comparison between the two targets in a common coordinate system. There is some evidence that directional GVS and CVS can alter visuospatial estimates: GVS impairs visually perceived vertical [44, 117, 175], and CVS can impair tasks employing complex visual mental imagery and mental rotation [118]. Vestibular sensing of gravity and whole-body orientation provides a valuable frame of reference for comparing spatial characteristics of internal and external cues [91], and is particularly relevant for interpreting visual stimuli with respect to the body (e.g., alignment) [20].

It may be that the dGVS-induced errors observed in Experiment 1 reflect an impaired proprioceptive position estimate for the left finger; however, it could also be the case that dGVS impairs the ability to convert the visual probe and finger position estimates into a common coordinate system. To test these possibilities Experiment 2 employed a non-visual finger orientation judgment task to see if dGVS-induced errors in left finger perception persist in the absence of a visual comparison task. I asked participants to report whether their finger was pointing to the left or right of gravity vertical (e.g., the direction a dropped brick would fall). I applied dGVS throughout the entire trial, including while the hand was moving and during the response phase.

If dGVS were to produce errors in proprioceptive localization of the left hand itself, then these errors should persist in a non-visual task. In this case I would expect an outwards rotation of the point of subjective equality (PSE) for the left finger while the participant experiences dGVS. This would correspond to a sense that the hand is rotated further inwards than veridical (as seen in Experiment 1), and must be tilted outwards to feel like it is aligned with gravity. See Figure 3.4, for a simple graphic demonstrating this. If, however, dGVS errors were specific to the line matching task described in the General Methods and in Experiment 1, I would expect to see no difference between dGVS and control conditions for either hand.

3.3.2 Methods

Participants

Thirteen participants (5 female, aged 21-62) participated in this experiment. All participants identified themselves as right-handed at the time of the study.

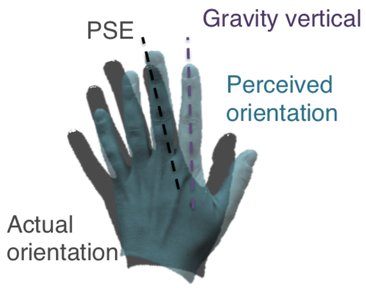

Figure 3.4: An illustration of how an inward-rotated perception of the left hand would produce an outward-rotated PSE. Participants' finger would need to be rotated outward of true gravity vertical to feel aligned with the direction of gravity. This image as a simplification assumes palm and finger orientation estimates are aligned.

Apparatus

The test apparatus was used in configuration A - "Frontoparallel" for this experiment (see Figure 2.1).

Procedure

Trials were as described in the General Methods, including distractor orientations. However instead of the final test orientation being chosen from a pre-selected set of orientations, it was chosen by a QUEST adaptive staircase [178]. The staircase was programmed to hone in on the 50% PSE between the finger being perceived as tilted to the right, or left, of gravity vertical (initial QUEST parameters: mean 0°, standard deviation 10°, grain 0.1°). Once their finger reached the final test orientation, no line appeared on the screen. Instead, participants were instructed to respond whether they felt their hand was tipping to the right or the left of the direction of gravity (i.e., the direction a brick would fall if it were dropped). They indicated their response using the left and right buttons on the mouse. Following response submission, the QUEST was updated and the mean of the new distribution function was used as the test orientation on the next trial.

The QUEST ran for 30 trials per block. Four blocks were tested in random order: the right and left hand with no stimulation, and the right and left hand with dGVS applied from onset of hand movement until participant response. The study took approximately 45 minutes to complete.

Data Analysis

Mean PSEs were calculated as the mean of the QUEST's distribution function after 30 trials. Each participant yielded four PSEs, one for each condition. Due to small sample size no values were identified as statistical outliers. A mixed model linear regression analysis was performed to determine whether stimulation (Control or dGVS) hand (left or right) and their interaction, significantly influenced PSEs. Degrees of freedom were corrected using the Sattherthwaite approximation [154]. Additionally, I conducted one-sample t-tests comparing PSEs in each condition to 0, to see whether perceived finger vertical was significantly different from true vertical in each condition.

3.3.3 Results

Mean group PSEs are shown in Figure 3.5.

The analysis found a main effect of hand, $F(1, 36)=20.95$, $p<0.001$. No other effects were significant. That is, I did not find evidence of an effect of dGVS on perception of haptic vertical. One-sample t-tests found that PSEs in both left hand conditions were significantly deviated from true vertical, $t(12)=-4.76$, $p<0.001$ (control), and $t(12)=-5.25$, $p<0.001$ (dGVS). Neither of the right hand PSEs significantly differed from 0 (p=0.6 or higher).

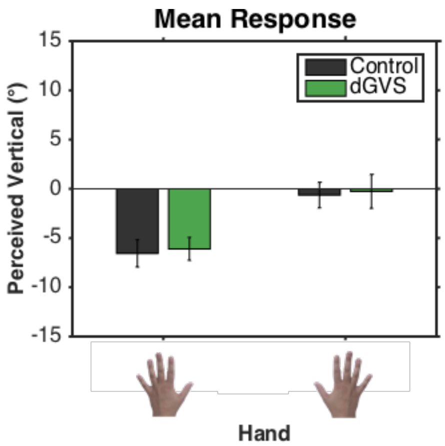

Figure 3.5: Mean PSE, or orientation at which the finger was perceived as aligned with gravity vertical, for each hand x stimulation condition. Error bars are standard error of the group mean.

3.3.4 Experiment 2 Discussion

In this experiment I sought to determine whether dGVS would rotate the PSE outward for left hand (indicating an inward rotation of perceived finger orientation). Both control and dGVS estimates of left finger orientation were rotated in the direction I anticipated, such that PSEs were significantly different from veridical. PSEs for the right finger in both conditions were no different from accurate.

There are two potential explanations for why I failed to find an effect of dGVS in this experiment. First, it could be that errors induced by dGVS in Experiment 1 were due to problems with converting proprioceptive (finger) and visual (probe) position estimates into a common coordinate system for comparison. In other words, in Experiment 1 participants may have been able to localize their left finger correctly, but could not report this accurately in a visual response task. In the non-visual orientation judgment used in this experiment, this reporting was not required and so dGVS did not influence responses. Yet this explanation cannot account for the systematic bias I observed in *both* left hand conditions in the non-visual response task in the present experiment.

A second possibility is that because the dGVS lasted substantially longer on each trial in this experiment, adaptation to the signal took place and the effect of dGVS on left hand perception was evident even in the control condition. Unfortunately, due to the small sample size and randomization of the trials, only one participant completed the left hand control condition prior to any dGVS conditions. Without further data it is difficult to speculate on the additive effects of dGVS and how this may have compromised the control conditions in this study.

The next study in this series repeats the line matching task in the transverse, or horizontal plane. Importantly, dGVS was applied throughout each trial in Experiment 3, making the length of stimulation time slightly longer than that of the present experiment. If the effects of dGVS are minimized in this experiment, it would suggest that the effects of dGVS in Experiment 1 were driven by the directional component of the short stimulations applied. If, however, an effect of dGVS reemerges, this would suggest that the lack of finding in the present experiment reflects a difference in task demands between Experiments 1 and 2.

3.4 Experiment 3: Perceived finger orientation in the horizontal plane is altered by disruptive Galvanic Vestibular Stimulation

3.4.1 Experiment 3 Introduction

Experiment 3 was motivated by two questions. First, do the hand-specific errors observed in Experiment 1 generalize to other planes of operation? Second, does the effect of dGVS in Experiment 1 reflect an effect of an induced illusory lean (created by playing only a short, 4s clip of the sum-of-sines signal) or is it a general consequence of vestibular disruption?

To answer these questions, I reorganized my experimental apparatus to the ”Horizontal” arrangement shown in Figure 2.1, and repeated the line-matching task. This horizontal configuration also allowed me to test a wider range of finger orientations (from -10° to 30°) due to the arm positions being more comfortable for the participant.. For the dGVS conditions, dGVS was started at the very beginning of the trial (prior to hand movement) and continued for the duration of the trial, until participants made their response. In the control condition, no dGVS was applied.

If this experiment were to replicate the findings of Experiment 1, it would suggest that the errors I had observed previously reflect errors in a hand-centric frame of reference that is unaffected by changes in the hands' position relative to the rest of the world. By contrast, a distinct set of errors would indicate that dGVS interfered with proprioceptive position sense in a highly context-sensitive way.

I also wished to explore the nature of the visual probe more thoroughly. In particular I was interested to know if the continued presence of the probe might “capture” responses, i.e., if the probe's orientation were to be inappropriately integrated into finger orientation estimates and thus had an influence on the final response [38]. I had reasoned that if this were the case, the longer the probe was visible, the more its position would influence finger orientation estimates, and the more erroneous those estimates would become. Upon further reading of the principles of sensory integration [37, 39], a problem in this logic became evident: to integrate two pieces of spatial information, a participant would have to make the assumption that they are linked to the same underlying event in the world. There is no reason to believe participants would do this with a line that is spatially close to, but causally distinct from, their actual finger. At that point however, data had already been collected to address this hypothesis, and analyses were performed on those conditions. In the interest of full disclosure I report the results of those conditions here.

3.4.2 Methods

Participants

Sixteen participants (12 female, aged 21-62, Mean age: 30 $\pm$ 10 years) participated in this experiment. All participants were tested on the Edinburgh Handedness Inventory (online edition, [22, 132]). Scores ranged from 55-100 (Mean value: 80 $\pm$ 10), indicating all participants were right-handed.

Apparatus

The test apparatus was used in configuration B - ”Horizontal” for this experiment (see Figure 2.1).

Procedure

Five test orientations were used in this study, ranging from -10° to 30° in 10° steps. Each test orientation was repeated 10 times in a block, resulting in 50 trials per block. Within-block trial order was randomly shuffled.

All participants completed two control conditions, one where the probe appeared at the start of the trial prior to hand movement (”continuous”) or after the hand reached the final test orientation (”follows”). They completed these conditions with dGVS triggered at the beginning of each trial. Participants completed each of these four blocks for each hand, leading to 8 experimental blocks total. Blocks were performed in a random order. Including instruction and set up, the experiment took roughly 1.5 hours to complete.

Data Analysis

Initial outlier analysis led to the removal of 16 pairs of accuracy and precision values. Of 640 total pairs of valid values, 624 were used in the analysis.

Accuracy values were analyzed in a mixed model linear regression, with the fixed effects of stimulation (Control, dGVS), hand (left or right), probe appearance (continuous or follows) and test orientation (-10°, 0°, 10°, 20°, 30°). Degrees of freedom were corrected using the Sattherthwaite approximation [154]. A second analysis was performed on precision values using the same parameters.

3.4.3 Results

Accuracy

Mean signed error for each of the conditions is shown in the top row of Figure 3.6.

I found a main effect of stimulation on signed error, $F(1, 234)=14.22$, $p<0.001$. Disruptive GVS significantly altered finger orientation judgments. The far right column of Figure 3.6 shows that this effect was a small but constant inward rotation of responses, across tested orientations. There was also a main effect of hand on signed error, $F(1, 234)=49.47$, $p<0.001$. Orientation judgments of the left hand were rotated inward compared to the right hand, for all conditions. I also found a significant effect of test orientation, $F(1, 234)=13.46$, $p<0.001$. Results show the characteristic compression of response orientations towards less extreme angles, also found in Experiment 1. Finally, no other main effects or interactions were significant. I did not find evidence that the presence of the probe during hand movement affected responses, nor did I find any selective effects of GVS on a particular hand.

Precision

Mean precision for each of the conditions is shown in the bottom row of Figure 3.6.

There were no significant effects of any of our dependent variables, or their interac-

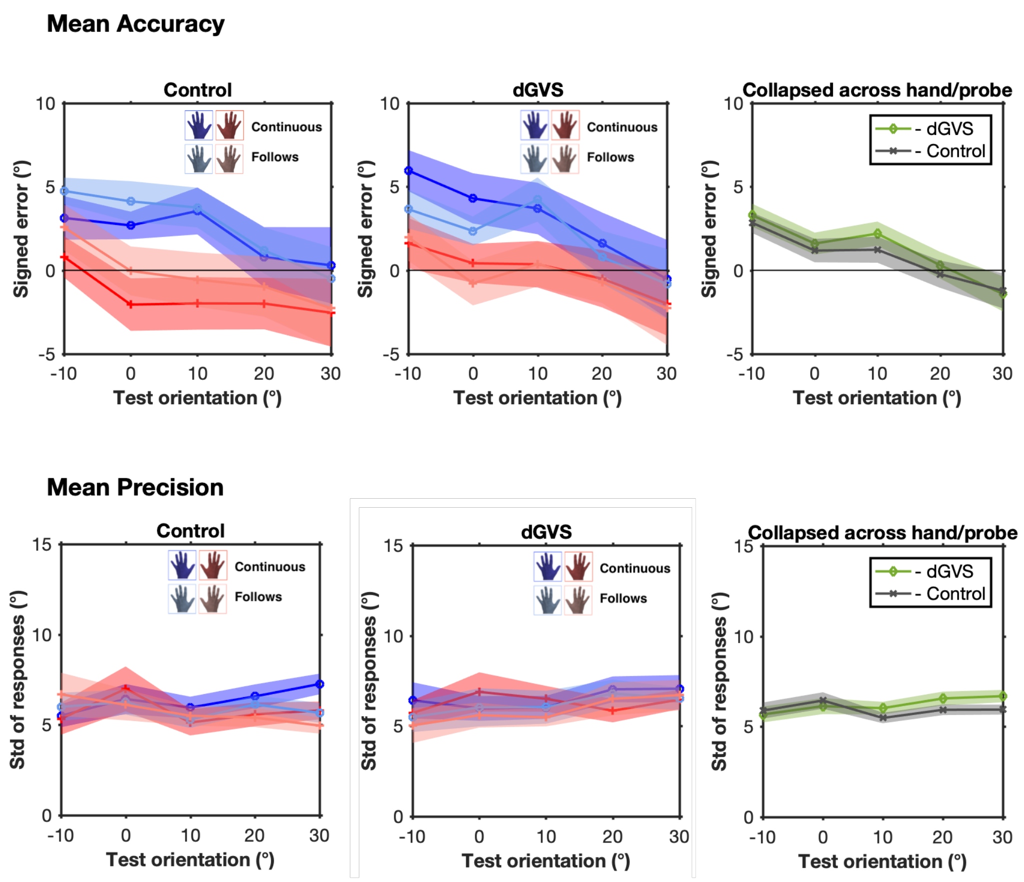

Figure 3.6: Top row: Mean signed error for each of the test orientations by stimulation condition. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Bottom row: Mean precision for each of the test orientations by condition. Shaded error bars are standard error of the mean.

tions, on precision of participants' responses (p=0.3 or higher).

Comparison to Experiment 1

Accuracy and precision for control and dGVS conditions are shown in Figure 3.7. I conducted a linear mixed model regression comparing the effects of plane of operation (frontoparallel or horizontal), stimulation (any dGVS condition, versus control conditions), hand (left or right) and test angle on signed error of response. I did not include data using the "continuous" probe from Experiment 3. I found a main effect of stimulation, $F(1, 589.67)=16.76$, $p<0.001$. There was also a main effect of hand, $F(1, 589.69)=31.87$, $p<0.001$, a main effect of test angle, $F(1, 589.67)=20.02$, $p<0.001$, a plane of operation x hand interaction, $F(1, 589.67)=15.85$, $p=0.016$, and a plane of operation x test angle interaction, $F(1, 589.68)=13.78$, $p<0.001$. No other main effects or interactions were significant. Taken together these results suggest dGVS has an influence on finger orientation estimates irrespective of plane of operation and hand. Finger orientation estimates, however, change as a result of hand, and tested angle, depending on the plane of operation.

A second linear mixed model compared the same factors as above for precision. There was a main effect of plane of operation, $F(1, 19.18)=19.90$, $p<0.001$; participants were significantly more precise in the frontoparallel position. There was also a main effect of hand, $F(1, 589.57)=3.99$, $p=0.046$. Participants were more precise for right hand orientation estimates, compared to left. No other main effects or interactions were significant.

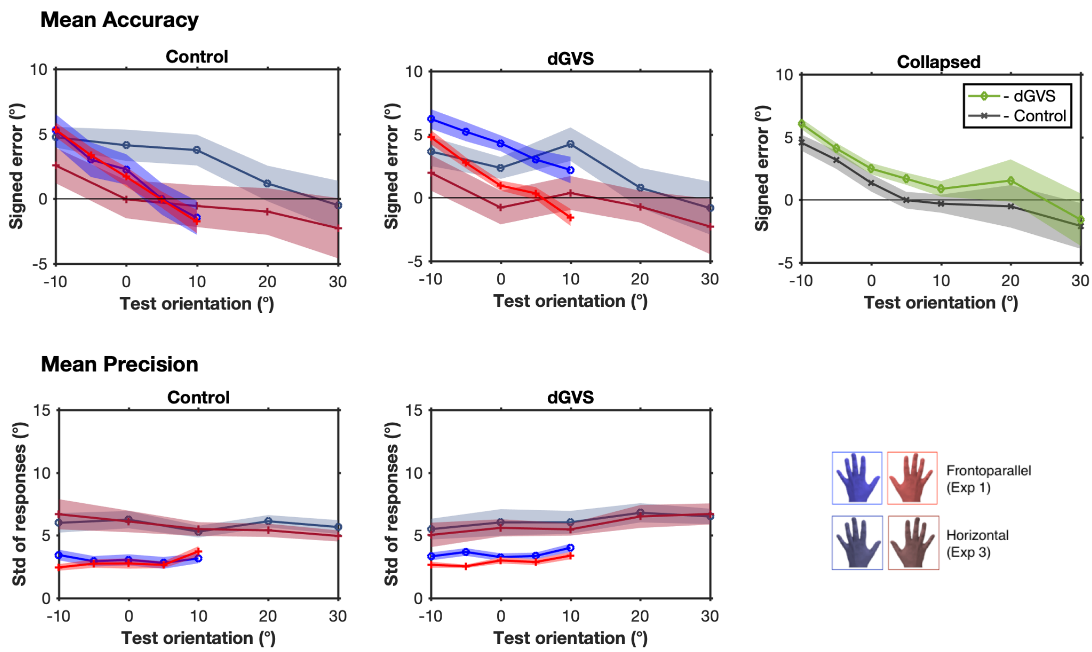

Figure 3.7: Top row: Mean signed error for each of the test orientations by stimulation condition, for the Frontoparallel (Exp 1) and Horizontal (Exp 3) planes. The rightmost graph shows the effect of dGVS collapsed across hand and plane of operation. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Bottom row: Mean precision for each of the test orientations by experiment. Shaded error bars are standard error of the mean.

3.4.4 Experiment 3 Discussion

In Experiment 3, I tested perceived orientation of the left and right index fingers using a line-matching task in the horizontal plane. I found that longer exposure to dGVS (19 s per trial) rotated orientation estimates inwards for both fingers. Critically, this longer exposure eliminated the possibility of the stimulation giving a consistent directional signal, which was a potential explanation for why I observed effects of dGVS in Experiment 1 (short exposure, possible directionality) and not Experiment 2 (longer exposure, no directionality). That I observed effects of dGVS in the present experiment strongly suggests the observed biases are not a reaction or adaptation to a directional signal, but instead are a response to the vestibular ”noise” of nondirectional GVS.

I also found an asymmetry in biases for the left and right hands, where left hand orientation estimates were biased more inwards than right ones, regardless of dGVS. I did not observe any significant differences in the precision of responses.

I also compared the results of Experiment 3 to Experiment 1. Two interesting results emerged. First, participants in Experiment 1 were substantially more precise than those in Experiment 2. This may reflect the smaller range of test angles used in this experiment, leading to narrower assumptions about possible finger orientations. Second, results indicated that finger orientation perception for the left and right hands changed as a result of the plane of operation. Specifically, when the palms were facing downward, an asymmetry appeared such that the left finger was perceived to be substantially rotated inwards of the right finger; when the palms faced outward, no such asymmetry was observed. These findings suggest errors in localization of body parts may be context- or pose-specific. This is a topic I will return to in Chapter 7, where I compare perceived finger orientation when the palms are facing up, or down, in the horizontal plane.

Why would the left and right finger perception be biased differently depending on how they're held? Ghilardi and colleagues have shown that perceived hand positions drift towards remembered workspaces [52]. It may be the case that holding the hands in different planes calls to mind different bimanual movements (e.g., hammering a nail vs. writing), and this association leads to different *a priori* assumptions about how the hands might be positioned. If it were true that top-down influences alter proprioceptive position sense, then training participants in certain hand orientations, or priming them with images of specific manual tasks, would shift observed biases in finger orientation perception. More research is needed in this area. For the moment, these data serve as a cautionary note to studies seeking to generalize orientation and position sense errors to multiple planes, or to some robust context-insensitive body map.

Disruptive GVS caused finger orientation estimates of both hands to rotate inwards. This is inconsistent with the pattern of results of Experiment 1, where only left hand estimates rotated as a result of dGVS. An analysis of the combined data from the two experiments found no plane of operation x dGVS interaction, suggesting that a failure to find an effect of dGVS on the right hand in Experiment 1 may have been due to a Type I error (effect was present but not significant). This effect may have become more pronounced with the longer exposure to dGVS in Experiment 3. Inward rotation of orientation estimate may reflect a response to the sense of instability and a drift towards positions of stability (e.g., bracing the hands inwards), or towards some canonical body position.

To extend these findings further, I completed one final experiment seeking to replicate Experiment 2, in the horizontal plane. Experiment 2 looked at finger orientation perception in a non-visual paradigm, where participants judged the orientation of their finger relative to gravity vertical. For Experiment 4 I used the non-visual target of ”straight ahead” of the body midline.

3.5 Experiment 4: Perceived pointing straight ahead with or without disruptive Galvanic Vestibular Stimulation

3.5.1 Experiment 4 Introduction

In Experiment 2 I showed that non-visual finger orientation judgments do not appear to be affected by dGVS. Taken together with Experiments 1 and 3, this suggests that the effects of dGVS may not be on finger orientation perception per se, but the ability to report this orientation in a visual line matching task. In this visual task, participants need to compare the proprioceptive position of their finger with the orientation of a visual stimulus, which requires converting one or both estimates into a common coordinate system. Disrupting normal vestibular function may lead to errors in converting proprioceptive and visually sensed information into a common frame of reference, as vestibularly-sensed body orientation is needed to help resolve external and internal spatial coordinate systems [91]. In contrast, non-visual tasks may not require the same kinds of transformations, remaining in proprioceptive or body coordinates to make the comparison between finger orientation and a target orientation. Yet as Experiment 3 demonstrated, evidence collected in one plane of operation may not generalize to other planes of operation. Experiment 4 therefore seeks to replicate the findings of Experiment 2, but in the horizontal plane.

Additionally, I included a novel dGVS condition where the dGVS signal began from a random place in the preset waveform (”dGVS-Random”). Until this point, all experiments triggered the dGVS from the beginning of the preset waveform (shown in Figure 3.1). While longer dGVS exposure times ($>$ 4 s) should have removed a persistent sense of directionality, a condition where the signal begins at random truly eliminates any consistency across trials. I also included a condition where the signal began from the start of the waveform (”dGVS-Restart”) for the purpose of comparison.

3.5.2 Methods

Participants

Twelve participants (8 female, aged 21-62, Mean age: 31 $\pm$ 12 years) participated in this experiment. All participants were tested on the Edinburgh Handedness Inventory (online edition, [22, 132]). Scores ranged from 55-90 (Mean score: 81 $\pm$ 9), indicating all participants were right-handed.

Apparatus

The test apparatus was used in configuration B - ”Horizontal” for this experiment (see Figure 2.1).

Procedure

Trials were identical to those described in Chapter 3 Experiment 2. Again the test orientation was chosen by an adaptive QUEST staircase on each trial. Participants were asked to report whether their finger was pointing left or right of ”straight ahead” from the middle of their body.

In addition to a control condition, and a dGVS condition where stimulation was triggered from the beginning of the sum-of-sines pattern at the beginning of each trial ("dGVS-Restart"), a new condition was included where dGVS was triggered at the beginning of the trial starting from a random location in the sum-of-sines program ("dGVS-Random"). Stimulation conditions were repeated with both hands, leading to 6 experimental blocks. Participants completed these blocks in a randomized order. The experiment took roughly 45 minutes to complete.

Data Analysis

Mean PSEs were calculated as the mean of the QUEST's distribution function after 30 trials. Each participant yielded six PSEs, one for each condition. Due to small sample size no scores were identified as statistical outliers. A mixed model linear regression analysis was performed to determine whether stimulation (Control, dGVS-Restart or dGVS-Random) hand (left or right) and their interaction, significantly influenced perceived straight ahead. Degrees of freedom were corrected using the Sattherthwaite approximation [154]. Additionally, I conducted one-sample t-tests comparing PSEs in each condition to 0, to see whether perceived finger straight ahead was significantly different from true straight ahead in each condition.

3.5.3 Results

Mean signed error for each of the conditions is shown in the top row of Figure 3.8.

The analysis found a significant main effect of hand, $F(1, 55)=46.90$, $p<0.001$. No other effects were significant. One-sample t-tests found that PSEs in the three left hand conditions were significantly deviated from true straight ahead, $t(11)=-5.06$, $p<0.001$ (control), $t(11)=-4.74$, $p=0.001$ (dGVS - Restart), and $t(11)=-12.13$, $p<0.001$ (dGVS - Random). None of the right hand PSEs significantly differed from 0 (p=0.7 or higher).

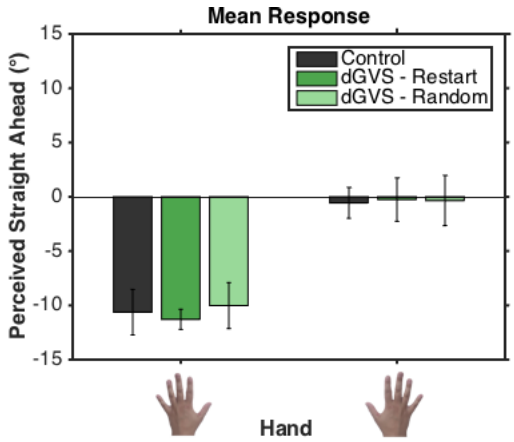

Figure 3.8: Mean PSE for pointing straight ahead, by hand and stimulation condition. Error bars are standard error of the group mean.

3.5.4 Experiment 4 Discussion

Experiment 4 sought to replicate the findings of Experiment 2 that dGVS does not appear to affect proprioceptive localization in a non-visual response paradigm, and extends that result to another plane of operation. The results of this experiment suggest that dGVS does not introduce a bias in proprioceptive localization of the fingers. Instead, dGVS appears to bias the comparison of proprioceptive orientation estimate to the visually-perceived orientation of the line. The vestibular system is valuable for sensory integration, particularly for comparing internal and external senses [91], and disrupting the perceived position of the body has been shown to interfere with visual imagery tasks and visual motion perception [32, 93]. Bresciani and colleagues demonstrated that directional GVS leads to deviations in reach trajectories to remembered visual targets, and suggested GVS may help maintain a sense of the spatial relationships between body parts and visual target locations [13]. My results here agree with this possibility, and further indicate these effects do not extend to comparisons between body parts and non-visual target orientations.

As part of this experiment I included a new condition in which dGVS was triggered from a random location in the dGVS waveform. Neither of the dGVS conditions had an effect on performance in this task. Anecdotally, while dGVS produces a general feeling of discomfort, participants reported that the dGVS-Random trials could be ”shocking.” This was a result of sudden changes in current running to the electrodes between the end of the previous trial and the start of the new one. Future studies should avoid this methodology, or implement a ramping up of the signal intensity at the beginning of a new bout of stimulation, to ensure participant comfort.

Finally, I found a bias in perceived pointing straight ahead for the left hand, but not the right hand. That is, the left hand was perceived to be rotated inwards of its actual position, which would entail a PSE that is rotated outward of true straight ahead. Figure 3.6 shows that left hand orientation estimates were biased inwards in the line-matching task as well, even in the control condition. I observed this effect for comparisons of finger orientation to vertical in Experiment 2 as well. This raises the interesting question of whether the left hand is perceived accurately in general. Indeed, to be able to understand how dGVS influences finger and hand orientation perception, it is necessary to have a sense of how this perception functions under ”typical” conditions. The rest of this dissertation focuses on how finger orientation perception operates during normal vestibular processing.

3.6 Chapter Discussion

Artificial vestibular disruption has been shown to alter both high-level and low-level features of body representation (see [107] for a review). In this Chapter, I presented a series of four experiments looking at the effect of vestibular disruption on perception of the orientation of the index fingers, while the hands were held palm-out (frontoparallel; Experiments 1 and 2) or palm-down (horizontal; Experiments 3 and 4). To assess orientation perception I used a visual line-matching task (Experiments 1 and 3), or a non-visual pointing judgment task (Experiments 2 and 4). In each experiment I included a control, no stimulation condition and at least one experimental condition where participants were subject to disruptive Galvanic Vestibular Stimulation (dGVS). DGVS is a form of electrical vestibular stimulation using an alternating sum-of-sines current, which produces a general sensation of instability that is both difficult to adapt to, and does not have a specific direction [112, 129]. In Experiment 1, I varied the timing of this stimulation (either before, during or after movement), and found no difference between the three conditions; in Experiments 3.2–3.4 I left stimulation on for the entirety of the trial. In Experiment 4, I also varied where in the sum-of-sines waveform the trial began; this did not differentially affect performance in the task.

Previous studies using directional forms of GVS and CVS (which can induce a sensation of leaning or swaying to one side) have found it can alter hand and arm perception both during movement and while stationary [13, 41, 108, 109, 115, 156]. In Experiment 1, I theorized that dGVS might impair 1) the ability to keep track of the position of the limbs, 2) disrupt an internal body map, or 3) both. I varied the time of stimulation such that dGVS was on while the spatial position of the body was being updated (during movement) or while the internal body map was most likely being accessed (during response). My rationale was dGVS would have the greatest impairment on performance if it were on while the vestibular system was being recruited. Thus, if the vestibular system was used to help keep track of the spatial position of the hands, dGVS should have the biggest impact if it was applied while the hand was moving; in contrast, if the vestibular sense were to help inform an internal map of the body, dGVS should have the greatest disruption while this map was being accessed, during response.

In fact dGVS significantly biased left finger orientation perception in all dGVS conditions, including an intended control condition where dGVS was applied before movement onset. Specifically, dGVS caused the perceived orientation of the left finger to rotate inwards, towards the thumb. I speculated that this selective influence could be an interaction between the sensation of instability and the role of the non-dominant hand as a stabilizer. In Experiment 3 I sought to replicate this effect while the hands were in a different posture (palm facing down), and I applied dGVS for the duration of the trial. In that experiment, dGVS created an inward bias for both fingers, compared to performance in the control conditions. Notably, this increased dGVS effect was accompanied by a decrease in precision for this experiment. These results are consistent with the possibility that longer exposure to dGVS can lead to increasingly impaired finger orientation perception. The inward rotation of orientation estimates is consistent with other research showing GVS shifts arm position estimates towards the midline [156], and shifts the locations of perceived touches towards the body [41], suggesting GVS may promote a general ”curling inward” of localization estimates towards the body.

Curiously, the dGVS-evoked bias I observed in the line-matching did not seem to persist in the non-visual matching task, where participants were asked to judge if they were pointing left or right of ”gravity vertical” or ”straight ahead” (Experiments 2 and 4). Both of these orientations may be coded in proprioceptive or body coordinates (e.g., a direction radiating up from the spine or out from the stomach). In contrast, the line-matching task required participants to compare the proprioceptively perceived position of their finger against a visual target, meaning they would have to take an extra step of converting these estimates into a common reference frame. My results suggest that dGVS may not impair proprioceptive position sense per se, but may interfere with the conversion of proprioceptive position estimates into visual estimates, or vice versa. The perceived orientation of the body is an important consideration when trying to convert internal position estimates into external coordinates [20]. Thus it may be that the vestibular disruption does not interfere with the tracking of the spatial location of the hands, or the internal body map, but rather with the ability to express these internal measures using spatial reference frames other than the body.

In the control conditions of several of the experiments in this series, I observed that the left index finger was perceived as rotated inwards of its actual position. This was in contrast to the perceived orientation of the right index finger, which was accurate in the non-visual tasks (Experiments 3.2 and 3.4). This finding was replicated for a line-matching task performed by right-handers in Chapter 4, in which there was no dGVS manipulation. However, I could not replicate it in the experiments in Chapter 5, and I will discuss the possible reasons why in that chapter.

One critical limitation of the studies in the present chapter is the absence of a between-subjects experimental protocol. Given that GVS may produce aftereffects [111, 175] and the nature of the aftereffects and repeated exposure to dGVS is not well known, it is not clear how much the presence of dGVS in this task may have influenced performance in the control conditions. In all experiments the order of conditions was randomized, and due to the small number of participants, order effects are difficult to discern. Even if participants completed the control condition first, they had electrodes attached to them at the beginning of the study; this may have primed them to behave in certain ways, or even tense their muscles, compared to in other experimental settings. Chapter 5 Experiment 2 shows how context and order effects may impact performance on the line-matching task. A between-subjects experiment, or a within-subjects design spaced over a period of at least a day, would be a valuable complement to the experiments reported here. In particular, it might illuminate whether the biases observed in the non-visual tasks, specifically for the left hand, persist when dGVS is not a part of the protocol. If biases do persist, it would be clear evidence that the perception of the orientation of the left hand/finger is different than that of the right, in right-handed individuals. If not, it would suggest that repeated dGVS may have considerable aftereffects following stimulation.

4 Handedness and haptic space

4.1 Introduction

In the previous chapter, I found that right-handed participants demonstrated an asymmetry in perceived orientation of the left and right index fingers, particularly in the horizontal plane. The present study had two distinct aims. First, I sought to determine whether these orientation perception errors would persist across multiple hand locations in space. Second, I wanted to compare finger orientation perception in left- and right-handed individuals, to determine whether handedness played a role in orientation perception errors. Both of these investigations were intended to further elucidate the source of observed biases in finger orientation perception. Specifically I was interested in whether these biases reflected errors in the representation of haptic space and/or the disproportionate representation of the dominant and non-dominant sides of the body.

A number of studies have demonstrated that haptic perception across reachable space is not veridical. This work has been pioneered by Kappers and colleagues [78–82, 153, 174, 184, 185], who examined haptic perception of the parallelity of pairs of bars across positions in space. Haptically-perceived parallel bars consistently diverge away from the body as the hands move laterally outwards. The authors have concluded in several papers that haptic space is non-Euclidean in nature.

Errors in the perceived position of the fingertip also appear to vary as a function of the hand's distance from the body. Rincon-Gonzalez and colleagues describe an experiment in which they moved participants' unseen hand to one of 100 target locations in a 2D plan in front of the body. After moving back to the start position, participants verbally reported the location where their fingertip had been. The authors found a high degree of individual difference in position estimation errors, but noted a group-level trend that position estimation was most accurate directly in front of the body [147].

Wilson and colleagues also mapped proprioceptive accuracy and acuity in a 2D horizontal workspace. In their task, participants had to report the location of their unseen, passively-moved hand with respect to either a remembered hand position, or a visual target. They also found the highest accuracy and acuity for hand positions close to the body, and further reported that at greater distances, the right hand was perceived more rightward of actual, and the left hand more leftward than actual. That is, location estimates diverged as the hands were moved farther from the body [179].

Both of the aforementioned studies on position sense used endpoint localization as a measure of perceived position sense. It remains unclear whether these localization errors reflect a rotation or a displacement. That is, I may perceive the *position* of my hand accurately, but if its perceived orientation were rotated outward from actual, consistent with a non-Euclidean haptic spatial sense, this would lead to mislocalization of the fingertip outwards. To my knowledge finger orientation as a function of position in space has not been systematically tested. In the present study, I conducted a blocked experiment where participants completed the finger orientation judgment task described in Chapter 3 Experiment 4, with the hands placed in front of the body midline, in front of the shoulder, or twice this width from the body midline. To expand upon the findings of the previous chapter, I used a wider range of test orientations to better capture the distribution of orientation perception across positions of the hand. Consistent with previous research on haptically-perceived orientation, I predicted orientation estimates would rotate outwards as the left and right hands moved away from the body. I further predicted that precision of responses would be worse for hand positions further from the body midline.

In addition to examining hand position, I also wanted to explore differences in perceived finger orientation between left- and right-handed individuals. Compared to right-handers, left-handers are more accurate in judging the length of their arms, and represent the space around their body more evenly [66]. Some evidence suggests that they are more accurate in sensing the position of their arms [156], although there is a surprising dearth of research on body and limb localization in left-handed people.

Right-handers show a dominant limb advantage for matching the hand to a visual location, and a nondominant limb advantage for replicating remembered joint angles [57]. This asymmetry is consistent with the dynamic-dominance theory of handedness, which suggests the dominant and nondominant limbs are specialized for precision control and stabilization, respectively, and show a preference for either endpoint position (manipulation) or relative joint angles (stability) as a result. [151, 152]. Some authors report that left-handers also show a nondominant limb advantage for matching joint angles [60], although other studies suggest left-handers are more varied in terms of the degree of asymmetry between the two limbs [143]. In Chapter 3, I observed an asymmetry in performance in my right-handed participants, where participants were on average more accurate and precise in their orientation estimates for the finger on their dominant hand. If this advantage were to reflect specialization for precision control, then left-handers may show a similar advantage for their left index finger.

Some authors have argued that left-handers may use different strategies for estimating limb position, such as pictorial representation of the body [50, 156], as a response to social pressures to use their nonintuitive, nondominant hand in everyday tasks. There is evidence that individuals with a considerable degree of practice visualizing their body parts (e.g., dancers) also have more accurate proprioceptive position sense [146], which may be why left-handers show improved performance in certain kinds of body perception tasks. Other authors have suggested that left-handers' more evenly distributed representation of the space around the body may reflect reduced hemispheric lateralization [143, 173]. Representations of the body in motor and somatosensory cortices are more evenly distributed across hemispheres in left-handers, compared to right-handers [86, 97, 164, 182]. Cortical areas related to body perception have been shown to expand with repeated use of a body part, as with musical training [36], which is consistent with a practice-based explanation for why left-handers might show less lateralization over time, although longitudinal studies on left-handers are needed to support this speculation.

If left-handers were less prone to asymmetries in dominant/nondominant body part representations, then I would expect reduced asymmetries between performance for both hands in left-handers, compared to right-handers. Alternatively, if left-handers were mirror opposites to right-handers in terms of hand specialization, then I would expect a dominant hand advantage in left-handers as well as right-handers. I could not find any studies on haptic perception of parallelity in left-handers; thus this experiment also serves as an exploration of whether orientation perception of the hands varies as a function of distance from the body in left-handers, as it does in right-handers.

4.2 Methods

4.2.1 Participants

Forty-one participants completed this experiment. Participant demographic information is listed in Table 4.1.

Group	n	Age: Range (years)	Age: Mean (years)	EHI Score: Range	EHI Score: Mean
Right-handed	21	17–40	22 ± 6	60–100	89 ± 13
Left-handed	20	17–24	19 ± 2	-100– -50	-86 ± 13

Table 4.1: Participant demographics for Chapter 4

4.2.2 Apparatus

The test apparatus was used in configuration B - "Horizontal" for this experiment (see Figure 2.1). In addition, participants were tested in three different body positions with respect to the apparatus: 1) with their hand directly in front of the body midline ("Midline" condition), 2) with their hand in front of the shoulder on the same side of the body ("Shoulder" condition) or 3) with their hand twice the distance from their body midline to their shoulder, away from the body midline ("Outside" condition). See Figure 4.1 for illustrations of these positions.

4.2.3 Procedure

Seven test orientations were used: -30° to 30° in 10° steps. Each test orientation was repeated 8 times in a block. Within-block trial order was randomly shuffled.

Trials proceeded as described in the General Methods section. All participants com-

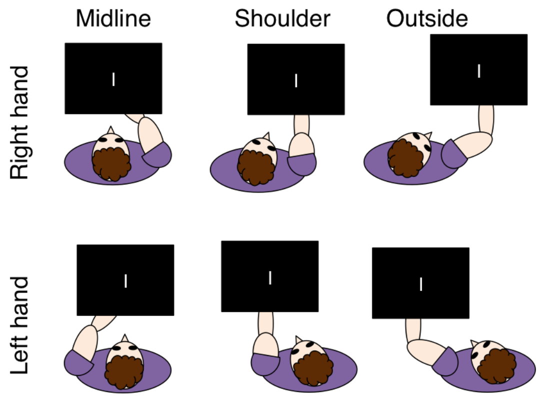

Figure 4.1: The three hand positions tested in experiment 1, shown for the right and left hands.

pleted blocks for the left and right hands at each of the test hand positions (midline, shoulder and outside). There were 6 blocks total, which were completed in a random order. In between blocks participants had the opportunity to view their hand while they moved to a new position. Participants arranged themselves by wheeling their chair so that their arm was in the correct position, with the aid of the experimenter. The apparatus remained stationary. Including instruction and set up, the experiment took roughly 1.5 hours to complete.

4.2.4 Data Analysis

Outlier analysis led to the removal of 21 pairs of accuracy and precision values. The removed data were from 8 of the 20 left handers, and the outlying scores were fairly dispersed across these 8 individuals. Of 1659 total pairs of values, 1638 were used in the analysis.

Accuracy values were analyzed in a mixed model linear regression, with the fixed effect of handedness (left-handed or right-handed), position (midline, shoulder, or outside), hand (left or right), and test orientation (-30°, -20°, -10°, 0°, 10°, 20° or 30°). Degrees of freedom were corrected using the Sattherthwaite approximation [154]. All factorial interactions were tested as well. A second analysis was performed on precision values using the same parameters.

4.3 Results

4.3.1 Accuracy

Mean signed error for each of the conditions for the two groups is shown in Figure 4.2.

The analysis found a main effect of position on signed error, $F(2, 1472.34)=162.75$, $p<0.001$. There was also a main effect of hand, $F(1, 1471.50)=15.95$, $p<0.001$, and a main effect of test orientation, $F(6, 1470.27)=5.19$, $p<0.001$. There was a significant handedness x hand interaction, $F(1, 1471.50)=30.18$, $p<0.001$. There was also a significant handedness x test orientation interaction, $F(6, 1470.27)=8.46$, $p<0.001$. Finally, there was a a significant position x test orientation interaction, $F(12, 1466.92)=3.04$, $p<0.001$. No other main effects or interactions were significant.

Taken together, these results demonstrate that: 1) for both right- and left-handers, responses deviate progressively more outwards as the hands move further away from the body midline, 2) right-handers are more susceptible to compression of responses towards the perceived centre of the tested range, compared to left-handers, and 3) right-handers show a clear difference in hands, similar to that of Chapter 3 Experiment 3, where the left hand's orientation estimates are rotated inwards from the right hand estimates. Left-handers did not show evidence of hand-specific orientation errors.

4.3.2 Precision

Mean precision for each of the conditions is shown in Figure 4.3.

The analysis found a main effect of position on precision, $F(2, 1469.49)=5.08$, $p=0.006$. A follow-up comparison found precision was significantly better at the shoulder vs. the outside, $F(1, 975.89)=9.42$, $p=0.002$, no other comparisons were significant. There was also a main effect of hand, $F(1, 1469.10)=4.66$, $p=0.031$, where the right hand was more precise than the left, and a main effect of test orientation, $F(6, 1468.88)=2.81$, $p=0.01$, which is further illustrated below. There was a significant handedness x hand interaction, $F(1, 1469.10)=8.01$, $p=0.005$. No other main effects or interactions were significant.

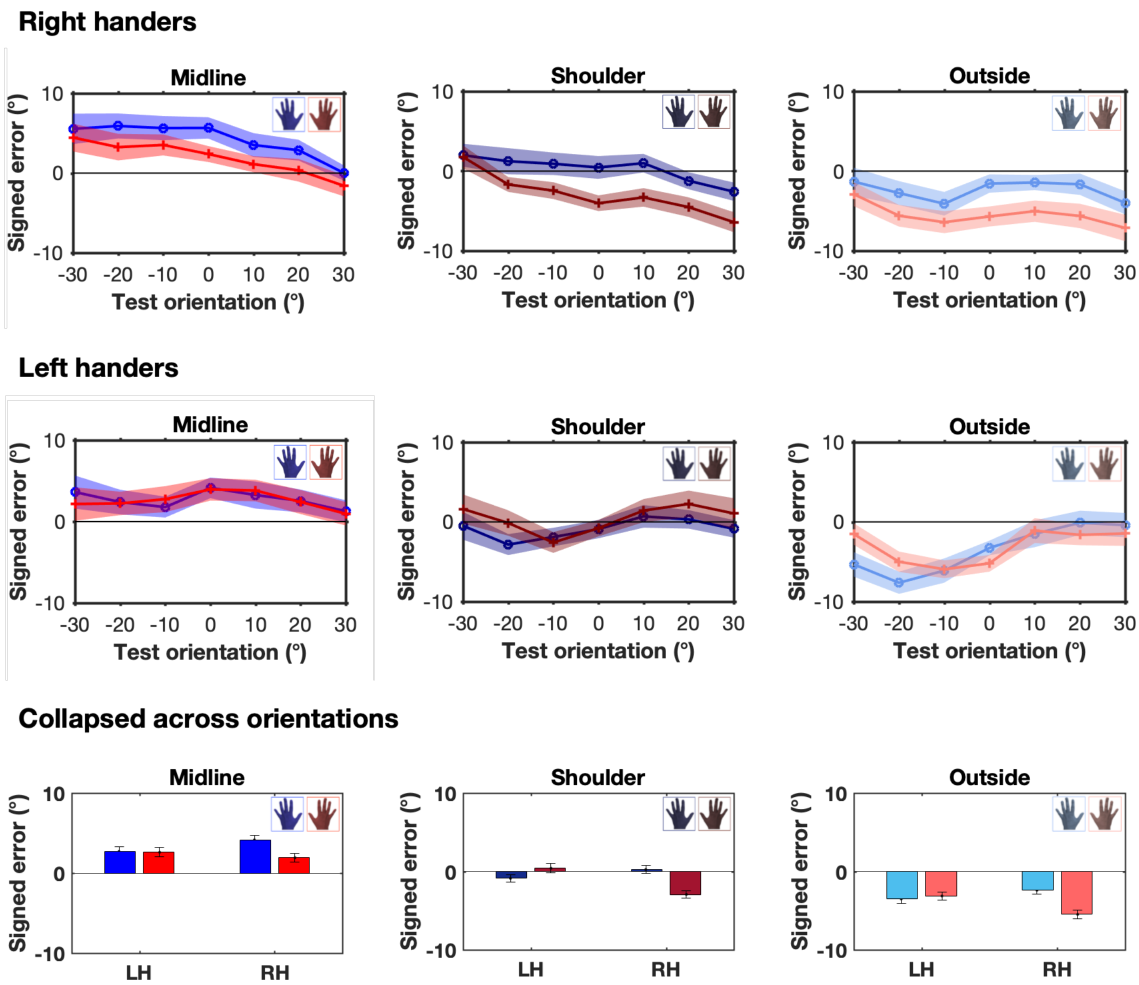

Figure 4.2: Top row: Mean signed error for the right-handed group, by hand position. Middle row: Mean signed error for the left-handed group. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Shaded error bars are standard error. Bottom row: Mean signed error for left-handers (LH) and right-handers (RH) collapsed across orientations. Error bars are standard error of the mean.

To further probe the interaction, I compared left vs. right hands in the two handedness groups separately. While there was a significant difference in precision between hands for left-handers $F(1, 1470.64)=11.90$, $p=0.001$, there was no difference between hands for right-handers. Another comparison looked at precision for the same hand across handedness groups and found that precision was different for the right hand between left- and right-handers, $F(1,45.04)=4.85$, $p=0.033$, while precision for the left hand did not significantly differ between the two groups. Figure 4.4 shows this interaction. Taken together, these results suggest that left-handers suffer a disadvantage in the precision of their orientation judgments for their non-dominant hand, while right-handers do not.

Finally, Figure 4.5 illustrates the main effect of test orientation on precision, collapsed across groups and conditions. Precision data from Chapter 3 Experiment 3 are included for comparison and show good agreement with the present data. Interestingly, participants show the most variability in responses for the straight ahead test orientation (0°).

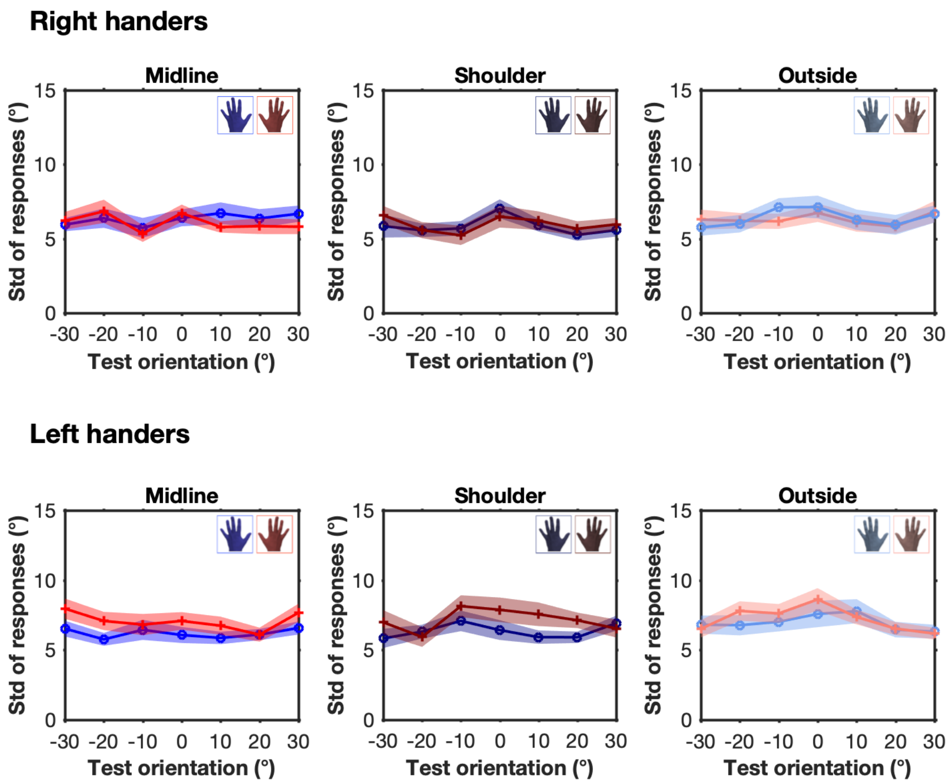

Figure 4.3: Top row: Mean precision for the right-handed group, by hand position. Bottom row: Mean precision for the left-handed group. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Shaded error bars are standard error of the mean.

4.4 Discussion

This study was based on two research questions: first, does perceived orientation of the fingers diverge as the hands move further away from the midline? And second, do left-handers show the same asymmetries in finger orientation perception as right-handers? To address these questions I conducted a block design experiment where participants completed finger orientation judgements by matching a line to the unseen orientation to their finger. They conducted this for several finger angles, with the left and right hands, with the hands positioned in front of the midline, in front of the shoulder, or twice this distance away from the midline. This

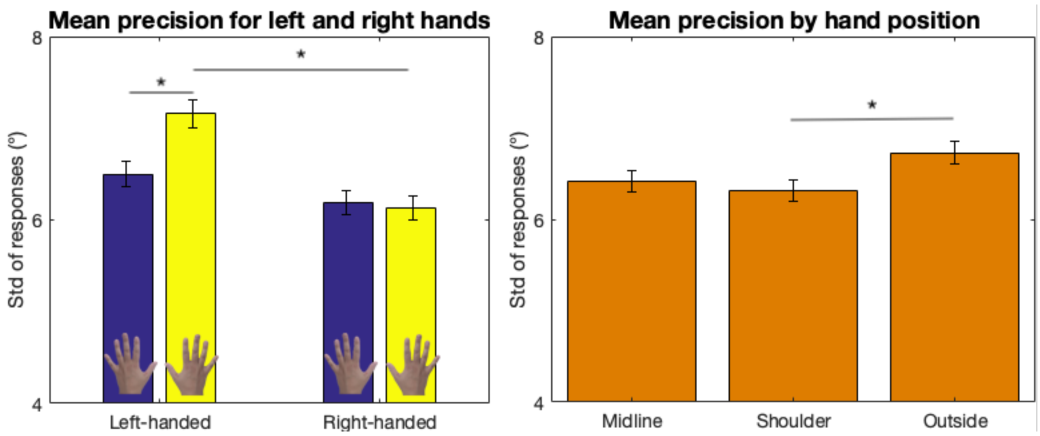

Figure 4.4: Left: Mean precision for the left and right hands, for both handedness groups. Right: Mean precision for each of the three hand positions. A * indicates $p<0.05$. No bar indicates a non-significant comparison. Note the scale of the y axis does not begin at 0.

experiment was completed with a group of right-handed and left-handed individuals.

4.4.1 Effect of hand placement on finger orientation perception

For both handedness groups, I found that at the midline condition, responses deviated inwards (towards the midline). As the hands moved further to the side, this bias rotated outwards, such that at the shoulder responses were largely accurate, and at the most lateral position biases were outwards (e.g., the right finger was perceived as rotated more rightwards, and the left finger was perceived as rotated more leftwards). Precision of responses for both groups increased once the hand moved past the shoulder position. These results agree with previous studies showing improved precision and accuracy of proprioceptive localization for spaces close to, and in front of, the body. They support the work of Kappers and colleagues showing that haptically-perceived orientations diverge outwards as the hand moves laterally away from the body [78–82, 153, 174, 184, 185], particularly outside the space in front of the body itself. My findings further extend this work by 1) showing that some of this effect may be due to misperception of the orientation of the effector itself (i.e., the fingers and hands), and 2) that this effect is present in left-handed individuals as well.

My findings are not in complete agreement with previous studies. While others report the fewest localization errors close to the body [147], I found that the finger orientation perception was best in terms of accuracy and precision, when the hand was placed directly

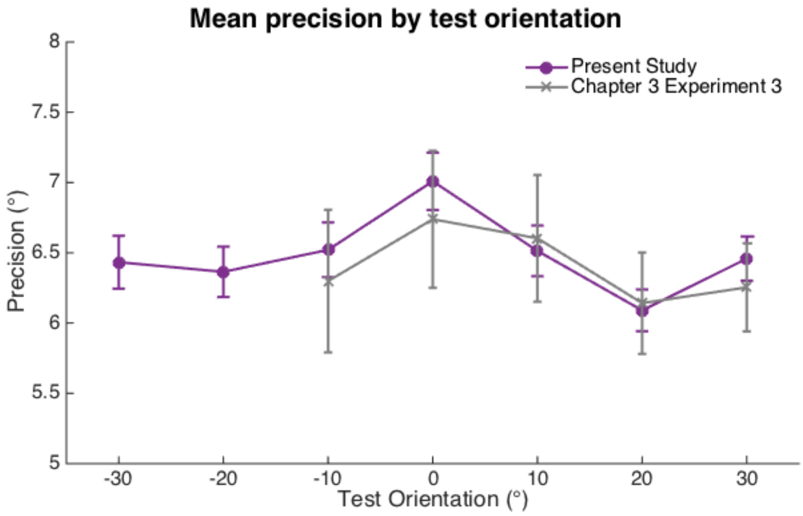

Figure 4.5: Mean precision by test angle for this experiment and Chapter 3 Experiment 3 (collapsed across other conditions).

in front of the shoulder. This may be due in part to the nature of the experimental setup: the 'close' positions in previous studies have been fairly natural in terms of the bending of the elbow, while the midline position in this experiment verged on uncomfortable for some of my participants. By contrast, the shoulder position was more natural, and reduced the number of joint angles and muscle flexion of the arm. This position is also close to what what Bromage and Melzack refer to as the "orthopaedic" resting state of the arm [14, 172], where the muscles are in a neutral, relaxed state. Van Beers and colleagues showed in an active arm matching task that greater muscle flexion/extension produced less precise responses, hinting that muscle strain may add noise to the proprioceptive afferent signal, increasing variability of responses [172]. Note that this may not be true for larger joints like the shoulder (cf. [165]). My results must be interpreted cautiously, however, as Chapter 5 shows that order effects, and the associated muscle conditioning of the different arm positions, may have exacerbated some of the errors observed in this study.

4.4.2 Effect of handedness on finger orientation perception

In Chapter 3, experiment 4 (horizontal configuration) I observed that right-handers were more precise and accurate when reporting the orientation of the finger on their dominant right hand, compared to their nondominant left hand. This effect may reflect the specialization of the dominant limb for precision control [151,152]. Some previous research on joint position matching suggests that left-handers may also show this dominant limb advantage [60] while other studies report reduced asymmetries in left-handers, both at the cortical and functional level [86, 97, 143, 164, 182], and overall more accurate arm position sense than right-handers [156]. In terms of accuracy, I observed an asymmetry in right-handers similar to what I found in Chapter 3 experiment 4, where the left hand was perceived as rotated more inwards of the right hand. By contrast, left-handers did not show any difference in terms of accuracy across their two fingers, and as a result were more accurate overall (see Figure 4.2). This is consistent with a more accurate representation of the two limbs in left-handers, and suggests the asymmetry observed in right-handers may be the result of increased hemispheric lateralization. Neuroimaging data is needed to demonstrate this on an individual level; my sample did not show enough variability in scores on the Edinburgh Handedness Inventory for a correlational analysis to be meaningful.

The precision analysis failed to replicate the finding in Chapter 3 experiment 4 that right-handers show a dominant hand advantage in precision of responses. Here, I found no difference between precision for both hands in right-handers, while left-handers showed a marked increase in variability of responses for their nondominant hand. I did not record the length of each trial across individuals, and so can only speculate, but this result hints at a conscious top-down influence, and a possible priming effect, on performance. Left-handers were recruited for this task specifically for their left-handedness, and completed the EHI prior to the line-matching task. Thus, they had been primed to consider their handedness abilities, and this may have affected the confidence with which they made judgments about their non-dominant limb. By contrast, being right-handed is a screening requirement for many studies on a variety of topics, and so may not have had the same priming effect on undergraduate right-handers with experience participating in research. I did not ask participants to report confidence levels in their responses, and I did not record the length of each trial, therefore this explanation is, at the moment, conjecture. Priming by calling attention to a person's minority status has an impact on spatial perception and cognitive ability [83, 122]. I could not find any experiments detailing whether priming a person to their handedness may impact limb position perception. Future experiments may benefit from asking participants to make confidence ratings about their responses and correlating these with variability in performance, and potentially using qualitative interviews during debriefing to further probe top-down influences on performance.

A novel finding of this experiment is that left-handers and right-handers show a similar outward rotation of finger orientation estimates as the hands are moved away from the body midline. To my knowledge, this is the first comparison between different handedness groups on this topic and suggests that some features of body and hand perception may be related to general spatial perception and not cortical lateralization or other handedness-specific factors. How left-handers explore and perceive haptic space is still a largely unexamined topic and merits further exploration. My results suggests that left-handed individuals may not differ from right-handers in performance in haptic parallelity perception and other tasks, which would be an interesting and valuable contribution to the literature, given other observed differences in how the two groups perceive and represent their bodies in space.

The study described in this chapter has a number of limitations. Chief among them are the nature of the display line (which was programmed such that it was more likely to appear to the inside of extreme angles), and the role of order effects. These topics form the basis for the next chapter, which explores how changes to the experimental paradigm itself can influence participant performance.

5 Methodological considerations

5.1 Chapter Introduction

In this chapter, I present two control experiments intended to explore the role of the display line and order effects on measurements of perceived finger orientation. As the outcome of these experiments affects the interpretation of the results outlined in several other chapters, I have included them as a distinct chapter in this dissertation.

Experiment 1 examines how the initial orientation of the visual line probe influences measurements of perceived finger orientation. In the previous chapter, the probe was programmed to appear in such a way that it was disproportionately rotated inwards for extreme test orientations (e.g., -30° and 30°). That is, participants were almost always rotating the line outward to reach the test orientation. Experiment 1 compared this line sampling method to three other methods, one an unbalanced uniform distribution with a wide range of possible orientations, one uniform distribution centred on the correct orientation with a wide range, and one based on a normal distribution about the correct response. The results suggest that the sampling method I used in the previous experiments may have exacerbated compression of responses towards the centre of the tested range. Furthermore, this display line sampling method showed asymmetries in errors and precision between the left and right hands. By contrast, more balanced sampling methods resulted in smaller asymmetries and a faster response time. The implications of this finding for other studies in my dissertation are discussed.

In Experiment 2, I revisited the findings of Chapter 4 regarding how the hand's position relative to the body influenced perceived finger orientation. In Chapter 4, there were 6 experimental conditions (3 hand positions x 2 hands) and the order of these conditions was randomized. The number of participants was such that only one participant completed all midline conditions before moving to the shoulder condition. Furthermore, that experiment used a display line sampling method which may have influenced results. In the current experiment, I used a more balanced display line sampling method, and systematically varied the order of the hand positions (between midline and shoulder positions only). I found that when participants completed the midline conditions first, they showed more compression of responses, and a large effect of hand position. By contrast, participants who completed the shoulder conditions first showed less compression and no effect of hand position. These results are discussed in the context of muscle conditioning and fatigue, and the role of comfort in participant responses.

5.2 Experiment 1: Perceived finger orientation is influenced by probe display parameters

5.2.1 Experiment 1 Introduction

In the previous experiments in this dissertation, participants reported perceived finger orientation by rotating a display line to align with the perceived orientation of their finger. To rotate this line, they pressed the left and right buttons on a computer mouse, which adjusted the line's position. In an attempt to mitigate the effects of hysteresis (i.e., the influence of the previous trial's finger orientation on current perception), I included a series of three motor movements at the beginning of each trial, such that participant's finger was rotated to three initial ”distractor” orientations before coming to rest at the test orientation. These distractors were randomly sampled from a normal distribution with a mean of the test orientation, and a standard deviation of 10°. This had the result that participants fingers could arrive at the test orientation from an inward or outward rotation with equal likelihood. A small caveat to this was that distractor orientations had to be between -40° and +40° to ensure participants' physical comfort.

By contrast, the display line's initial orientation when it appeared on screen, was not equally distributed around the test orientation. For previously described experiments, the line's initial orientation was randomly sampled from a uniform distribution from -10° to +30°. This had the unintended consequence that for extreme inward and outward test rotations, participants almost always rotated the line from the same direction. For a visual depiction of this see Figure 5.1, which shows the distributions of repeated sampling of the display line; the actual test orientation is shown in red. If perceived finger orientation were a normally-distributed estimate, and participants stopped rotating the line when they felt it was close enough to their internal estimate, then always rotating the line from the same direction could introduce an error in that direction [51]. Such a bias would be characterized by an inward bias for extreme outward angles and an outward bias for extreme inward angles. Indeed, I consistently observed this compression of responses in my previous experiments, at least for right-handed individuals.

The following experiment examines how the sampling method for the probe's initial orientation might influence participants' responses in my paradigm. I compared random sampling from three uniform distributions: the original -10° to 30°, a wider -40° to 40° that encompassed the entire test orientation range, and a distribution with a range of 80° and a mean of the test orientation. I included a fourth condition where the initial display line was sampled from a random normal distribution with a mean of the test orientation and a standard deviation of 10°. Figure 5.1 shows a series of histograms of the initial line orientation for 5000 samples using each of the four methods, for each of the test orientations used in this and the previous chapter. I hypothesized that the two distributions not centred on the test orientation (-10° to 30° and -40° to 40°) would show greater compression of responses towards the centre of the test range, and this compression would be greatest for the condition with the smallest range. The two centred conditions were included to determine whether my previous findings (left finger rotated more inward than right, partial evidence for better precision with the right hand) could be replicated using a more balanced psychophysical paradigm. Finally, I included a new measure of performance, trial response time, to capture differences between measured perception of the two hands across sampling conditions. I hypothesized that the uniform distributions would result in longer response times, increasing with the size of the range.

5.2.2 Methods

Participants

Eighty-four participants completed this experiment. Participant demographic information is listed in 5.1.

Display Type	n (f, m)	Age: Range (years)	Age: Mean (years)	EHI Score: Range	EHI Score: Mean
-15 to 30	20 (18, 2)	17–39	22 ± 6	50–100	86 ± 13
-40 to 40	26 (20, 6)	17–22	19 ± 1	60–100	87 ± 12
80 centred	21 (17, 4)	18–51	22 ± 8	65–100	87 ± 12
Normally distributed	17 (10, 7)	18–34	20 ± 4	60–100	89 ± 15

Table 5.1: Participant demographics for Chapter 5 Experiment 1

Apparatus

The test apparatus was used in configuration B - ”Horizontal” for this experiment (see Figure 2.1). Participants were all tested with their hand placed in front of their shoulder, similar to the ”shoulder” position described in the previous chapter.

Procedure

Seven test orientations were used: -30° to 30° in 10° steps. Each test orientation was repeated 8 times in a block. Within-block trial order was randomly shuffled.

All participants completed blocks for the left and right hands with the hand positioned directly in front of the shoulder. In some instances, participants completed these blocks as a part of a larger study. For example, some of these data are from participants who completed experiment 2 described in this chapter. To avoid the possibility that other blocks in those studies influenced the data presented here, I only included data from participants who completed the left and right hand blocks for the shoulder position *prior to any other experimental blocks* in the study they were a part of.

Trials proceeded as described in the General Methods section. The key difference between the four experimental conditions was the initial orientation at which the probe appeared. In the "-15 to 30" condition, the probe could appear at any orientation between -15° and 30° (in inwards–outwards coordinates), with equal likelihood. In the "-40 to 40" condition, the the probe could appear at any orientation between -40° and 40° with equal likelihood. In the "80 centred" the probe could appear at any orientation ± 40° from the test orientation with equal likelihood. Finally, in the "normally distributed" condition, the probe was randomly drawn from a normal distribution with a mean of the test orientation, and a standard deviation of 10°, using the MATLAB randn.mat function.

Figure 5.1 shows the results of a simulation where probe orientations were sampled 5000 times at each test orientation. The graphs display histograms of the frequency of test orientations displayed. This figure illustrated the balanced or unbalanced ratios of likely probe orientations in each experiment.

Finally, a junior research assistant was stationed in the testing room during the course of the experiment. This research assistant did not speak to the participant during testing blocks.

Data Analysis

Outlier analysis led to the removal of 16 pairs of accuracy and precision values. Of 1176 total pairs of values, 1160 were used in the analysis.

Accuracy values were analyzed in a mixed model linear regression, with the fixed effect of display type (-15° to 30°, -40° to 40°, 80° centred or normally distributed), hand (left or right), and test orientation (-30°, -20°, -10°, 0°, 10°, 20° or 30°), and the intercepts as a random effect. Degrees of freedom were corrected using the Sattherthwaite approximation [154]. Analyses using the same parameters were performed for the dependent variables of precision and response time. Finally, a correlation analysis between response time and precision and signed error was performed to determine whether response time was related to my standard measures of performance.

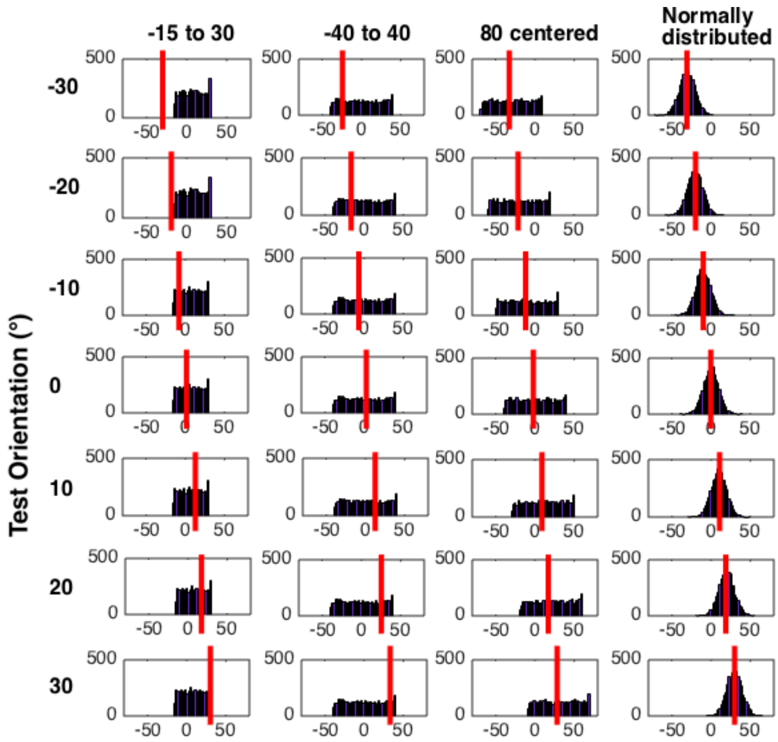

Figure 5.1: Results of a simulation where probe orientation was sampled 5000 times for each tested orientation, using the four different display types described in the Procedure. Histograms show the frequency of a given probe orientation given the display program. The red line indicates the actual position of the test orientation. This figure demonstrates how different methods of probe orientation selection can result in a different, potentially uneven likelihood of the probe appearing tilted inwards or outwards of the test orientation.

5.2.3 Results

Accuracy

Mean signed error for each of the four display types is shown in the top row of Figure 5.2.

There was a main effect of hand, $F(1, 1031.53)=25.96$, $p<0.001$. Across conditions, orientation estimates for the left hand deviated outward compared to the right hand, see Figure 5.3. There was also a main effect of test orientation, $F(6, 1027.24)=7.04$, $p<0.001$. There was a significant display type x test orientation interaction, $F(18, 1027.31)=2.34$, $p=0.001$. No other main effects or interactions were significant. A follow-up analysis assessed the effect of display type at each of the test orientations, and found that there was a significant main effect of display at the two extreme orientations, -30° $F(3, 459.07)=2.95$, $p=0.032$, and 30°, $F(3, 450.37)=3.21$, $p=0.023$. The effect was not significant at other test orientations. Mean signed error by test orientation is shown for each of the display types, collapsed across hands, in Figure 5.4. The compression effect is clearly evident for the -15° to 30° display type, which was what was employed in my previous studies.

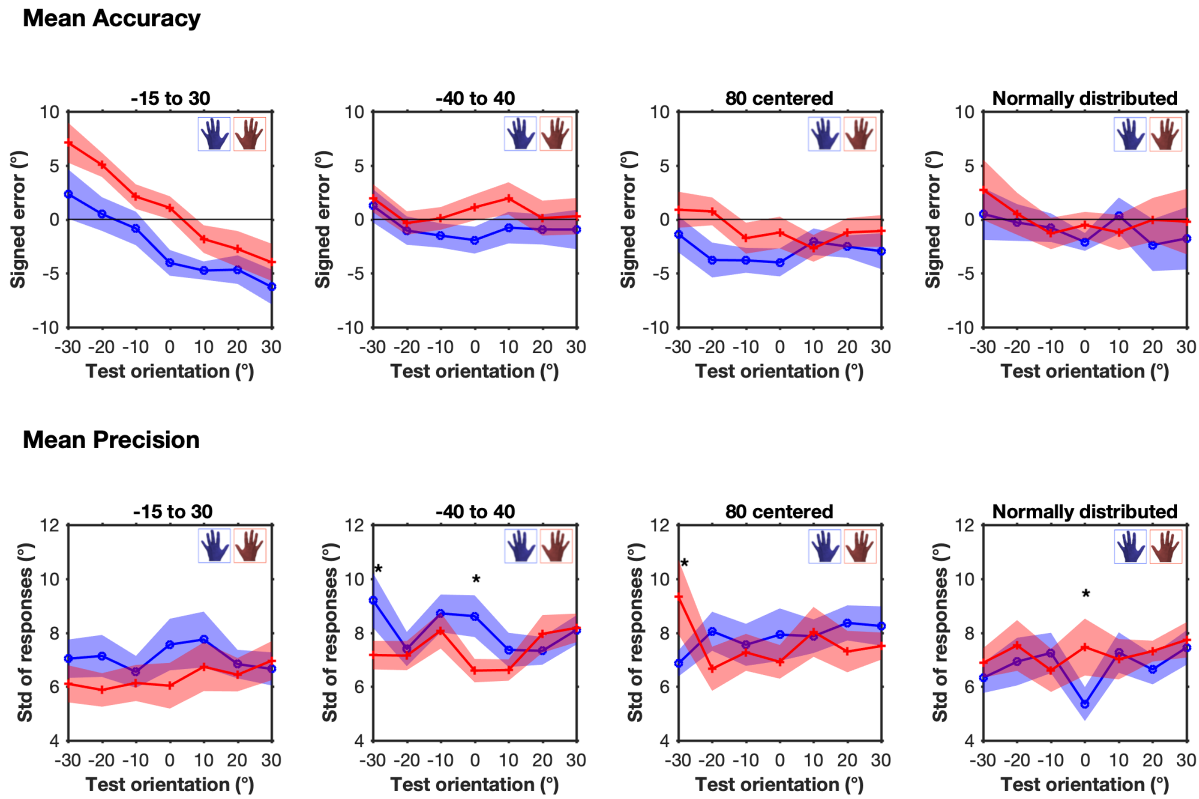

Figure 5.2: Top row: Mean signed error for the four display types, separated by hand. Bottom row: Mean precision of responses. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Shaded error bars are standard error. An asterisk indicates where there is a main effect of hand for that test orientation/display type (precision analysis only) $p<0.05$.

Precision

Mean precision for each of the four display types is shown in the bottom row of Figure 5.2.

The main effect of hand was significant, $F(1, 1024.33)=3.87$, $p=0.049$. There was a significant display type x hand interaction, $F(3, 1024.35)=2.99$, $p=0.030$. There was also a significant three-way interaction between the display type, hand and test orientation, $F(18, 1024.31)=1.79$, $p=0.022$. Follow up comparisons found precision was worse for the left hand for the unevenly distributed displays, $F(1, 1024.15)=5.57$, $p=0.018$ (-15° to 30°), and $F(1, 1025.02)=6.08$, $p=0.014$ (-40° to 40°), while there was no difference in precision for both

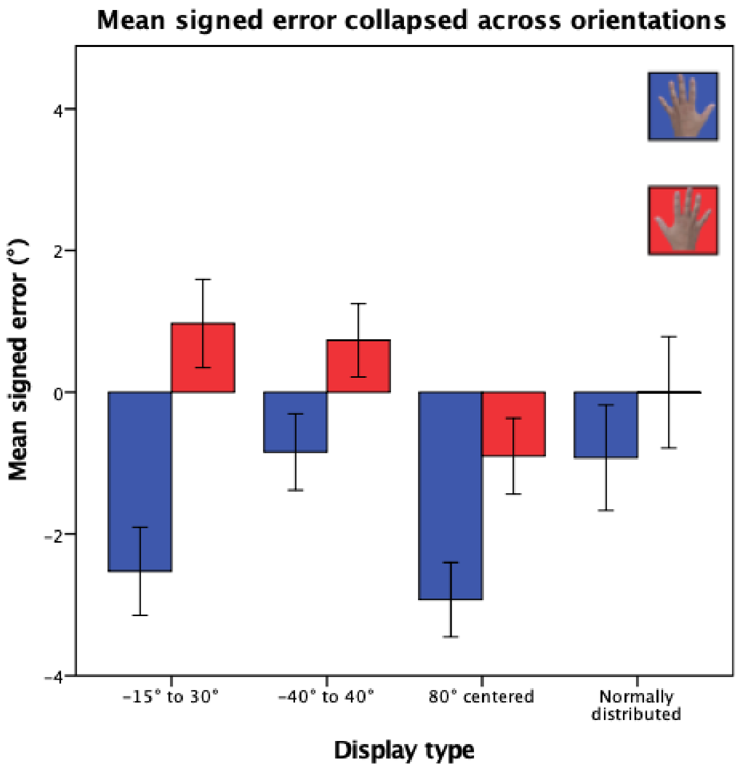

Figure 5.3: Mean signed error for the four display types, collapsed across test orientations. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Error bars are standard error of the mean.

hands for the other two display types (p=0.17 or higher).

To explore the 3-way interaction I looked at main effects of hand for each test orientation separated by display type. The only significant differences were: -40° to 40°, -30° condition (F(1,1025.90)=7.80, p=0.005); -40° to 40°, -0° condition (F(1,1026.066)=6.30, p=0.012); 80° centred, -30° condition, (F(1,1024.15)=9.16, p=0.003); and Normally distributed, 0° , (F(1,1024.15)=5.41, p=0.02). These differences are marked with an asterisk in Figure 5.2, though they are not in a consistent direction.

Overall, the precision analysis showed that the display sampling method influences precision of orientation perception for the left hand, particularly when the task is vulnerable to probe-driven response errors. However, some variability in performance exists across specific test angles within display conditions.

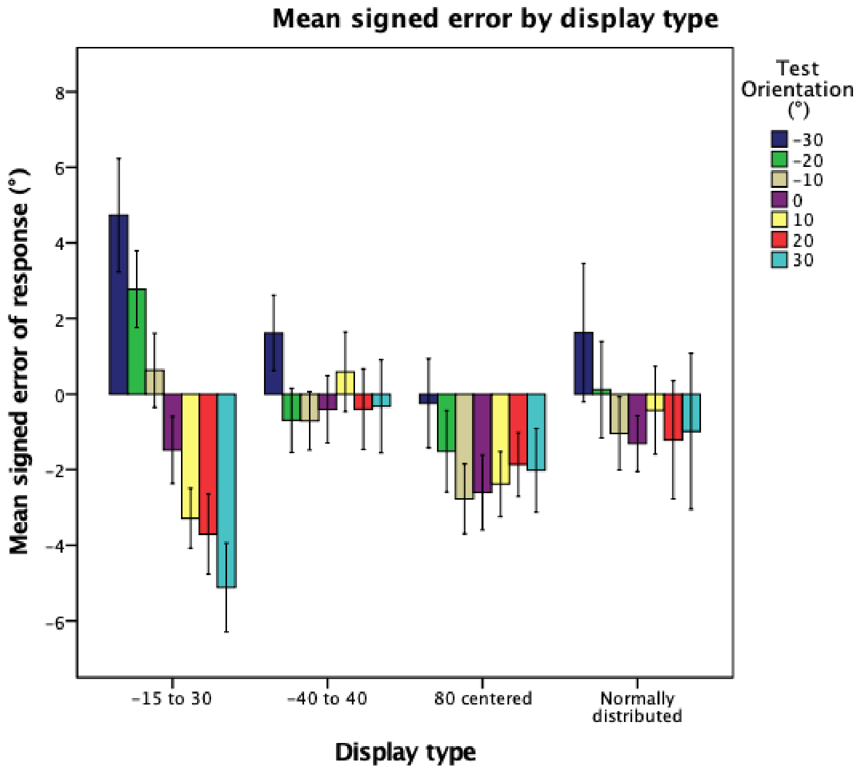

Figure 5.4: Mean signed error for the four display types, separated by test orientations, and collapsed across hands. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Error bars are standard error of the mean.

Response time

Mean response time for each of the four display types is shown in Figure 5.5.

There was a main effect of hand, $F(1, 1023.03)=5.64$, $p=0.018$. Participants responded faster for orientation judgments made regarding the left hand. There was also a main effect of display type $F(3, 79.97)=3.66$, $p=0.016$, and a main effect of test orientation $F(1, 1023.05)=26.31$, $p<0.001$. There was a significant display type x test orientation interaction, $F(18, 1023.06)=6.23$, $p<0.001$. Figure 5.5 indicates that participants took longer to make responses when the probe line had a higher likelihood of starting at an initial orientation quite far from the test orientation. No other effects were significant.

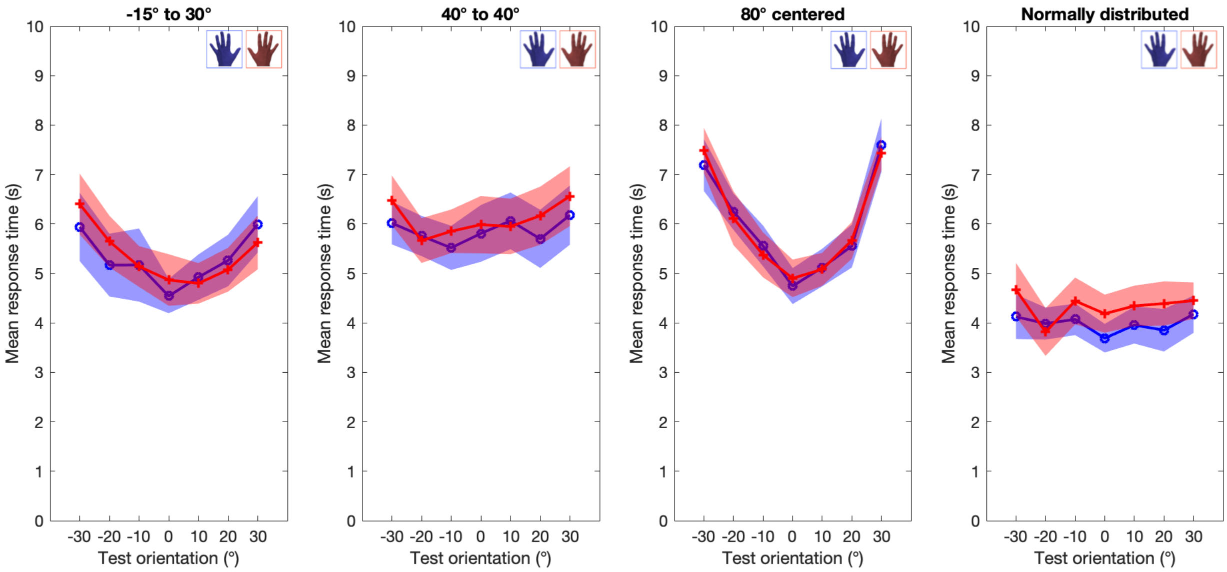

Figure 5.5: Mean response time for each trial, for the four display types. Shaded error bars are standard error of the mean.

Correlations

Response time was not significantly correlated with either precision ($r(1159)=0.005$, $p=0.87$) or signed error ($r(1159)=0.004$, $p=0.89$).

5.2.4 Experiment 1 Discussion

This experiment explored whether the effects I observed in my previous experiments were influenced by the characteristics of the display line I used as a response probe. Due to the programming of the display, the probe was disproportionately likely to be tilted inwards of extreme inward/outward test orientations. I had hypothesized that this problem may have led to an increased ”compression” of responses towards the centre of the sampling range for the initial line orientation. The results of the present study supported this hypothesis and suggested that the characteristic steep slope of orientation biases I observed in Chapters 3 and 4, with outward orientations being biased inwards, and inward orientations being biased outwards, was due in part to the nature of the test probe. The unbalanced display method also resulted in less precise responses for the left hand compared to the right hand.

As the sampling methods became more balanced, this slope of estimation errors became more shallow, and precision became more even between the two hands. A uniform sampling method centred on the correct response produced a smaller discrepancy in bias between the two hands, but an overall outward bias and a U-shaped distribution of response times, with more extreme angles leading to longer response times; this may have been due to participants rotating the line entirely around when responding to extreme positions. A sampling method based on a normal distribution about the correct response produced the smallest asymmetries and the fastest response times.

The condition which used my former sampling method (-15° to 30°) did not completely replicate the bias I observed in the previous two chapters. Previously I consistently showed left hand estimates were rotated more inwards than right hand ones, with a compression of responses towards the centre of the test range. While I observed a similar compression effect here, left hand estimates were rotated more outward of right hand estimates. Right hand errors in this experiment were similar in direction and magnitude to the “shoulder” condition of Chapter 4, suggesting perceptual errors for the left hand specifically were not replicated. This surprising finding has no clear explanation, as considerable pains were taken to make this experiment as methodologically similar to that previous condition as possible. Two outstanding differences are discussed below.

First, in this experiment a junior research assistant sat with participants in the room during the experiment, to observe performance. This was not the case in the previous study. This assistant did not speak to participants during the task; nevertheless, it is possible that their presence in the test room altered participant behaviour, either by causing them to put more effort into the experiment while under observation, or alternatively by providing a distraction. Why this might lead to different perceptual errors for the left hand is not clear, only that it may have elicited different strategies for response. To expand on this, if biases towards the centre of the line orientation sampling range reflect a strategy of “stopping when I’m close enough,” (strategy A) then a more effortful strategy might be “stopping when I’m certain I’m in the right spot” (strategy B). These strategies vary in the degree of confidence required to submit a response. In terms of the distribution of the internal estimate of the participant’s finger orientation, strategy A might lead participants to stop, for example, one standard deviation before the mean of that internal estimate. Strategy B, which requires a higher degree of confidence, might lead participants to stop at the mean itself, or even past it, when they are approaching the sense that they’ve gone too far. I might expect differences in response strategy to be reflected in response time data, but I did not record response times on a trial-by-trial basis in previous studies, and so I cannot make a direct comparison. The explanation of different strategies requires further empirical support– explicitly instructing participants on different strategies for performing the task, or providing different levels of external motivation through incentives and encouragement, would be useful for exploring these effects further. Response time data may also help illuminate differences in how participants are approaching the task.

A second difference between this experiment and Chapter 4 is the length of the study. The data obtained in the previous chapter were part of a 1.5 hour long study, and the line task studies in Chapter 3 were similarly quite long. If an inwards bias represents a strategy of "stopping when I'm close enough," this may have been exaggerated by participant fatigue. By contrast, a shorter study may result in different response strategies, such as overshooting. More data and targeted experimental conditions are needed to support this explanation.

Overall, this experiment demonstrated that the initial orientation of the probe line was an important factor in performance on this task. My results serve as a caution for future experimental design, although they show an interesting result specifically between the two balanced line sampling strategies (80° centred and normally distributed). Both of these methods can be considered psychophysically sound methods of line orientation sampling, but produce different degrees of error and response times. In the next experiment in this chapter, I use the 80° centred method to examine possible order effects in hand placement and perceived finger orientation. I specifically chose this methodology as it is a) balanced and b) still shows some asymmetries between the two fingers, which I wanted to explore. In the next two chapters I use the normally distributed sampling method, as it allows for faster responses and reduces the asymmetries I observed in unbalanced and uniform sampling techniques, allowing me to target other effects.

5.3 Experiment 2: Order of hand placement affects perceived finger orientation

5.3.1 Experiment 2 Introduction

In the studies described in previous chapters, I tested hypotheses regarding how participants' perceived finger orientation can change as a function of: vestibular disruption, plane of operation, handedness, hand position and initial probe line display characteristics. Errors in fingertip localization can vary across individuals, although group-level trends are still evident [147]. There is also evidence that certain kinds of training, like dance, can improve limb position sense [146]. I anticipated some level of inter-individual variability in performance on my task. In order to reduce variability between conditions, and to specifically target factors modulating finger orientation perception within an individual, in almost all of these studies I elected for within-subjects designs. However, as I noted in Chapter 3, the length of these studies introduces problems of adaptation, fatigue and muscle conditioning, all of which have been shown to influence arm localization [2, 27, 52, 176]. In the current study, I examine how order of a subset of hand placement conditions from Chapter 4 might affect finger orientation perception.

In Chapter 4, participants completed the line-matching task with their left or right hand. I positioned the tested hand directly in front of the body midline, in front of the shoulder, or at twice this distance to the outside. These positions, particularly the midline and outside conditions, could put strain on the muscles of the hand and arm. Contracting and relaxing a muscle without changing its length, as one might do in order to maintain a fixed arm position while the wrist is rotating, has been shown to lead to subsequent biases in the perceived position of the arm in the direction opposite flexion [141, 180]. As a muscle is continuously exercised, arm localization drifts in the direction opposite flexion, suggesting participants continue to think that their muscle is more lengthened than it actually is [2, 176].

Though I did not measure muscle activity directly in Chapter 4, a natural consequence of the hand positions I tested was a difference in muscle strain across conditions. While in the shoulder position, participants' upper arms were relatively relaxed across the full range of text orientations. At the midline position, however the bicep was contracted in order to keep the arm positioned in front of the body. If there were an effect of upper arm muscle conditioning on finger orientation perception, completing the midline condition immediately prior to a shoulder condition might lead to subsequent outward rotational bias of responses. Because I randomized the order of the six experimental conditions for each participant in Chapter 4, I did not have a great deal of statistical power to isolate and examine effects of muscle strain across individuals, between conditions. Therefore, I conducted a follow-up study where participants completed both midline arm positions, followed by both shoulder positions, or vice versa. Consistent with other research showing that muscle conditioning can lead to biases in the direction opposite flexion, I predicted that participants who completed the midline condition first would show increased outward rotational errors in the subsequent conditions, compared to when the conditions were reversed and participants did not experience muscle strain in the first block.

The study I describe here examines how order effects may have led to distinct biases in the data. Because these data use a more balanced line orientation sampling method (80° centred, see experiment 5.1), and because the results have general implications that can affect the interpretation of many studies, I am reporting the results Chapter 5 (dedicated to methodological concerns) as opposed to in Chapter 4.

5.3.2 Methods

Participants

Thirty-nine participants (29 female, 10 male) completed this experiment. Participant age ranged from 17-51 with a mean of 21 years $\pm$ 6. Participants all scored between 60 and 100 on the Edinburgh Handedness Inventory [22, 132], indicating they were all right handed. The mean EHI score was 86 $\pm$ 13.

Apparatus

The test apparatus was used in configuration B - ”Horizontal” for this experiment (see Figure 2.1).

Procedure

As in experiment 1, seven test orientations were used: -30° to 30° in 10° steps. Each test orientation was repeated 8 times in a block and within-block trial order was randomly shuffled.

Trials proceeded as described in the General Methods. All participants completed blocks for both hands with the hands positioned 1) directly in front of the body midline, and 2) directly in front of the shoulder. While the order in which the hands were tested was randomized, the two midline blocks were either the first two tested blocks ("midline first") or the last two blocks ("shoulder first"). Thus while all participants completed four blocks, order of hand position was a between-subjects factor. Participants changed hand position by wheeling the testing chair so the apparatus was positioned in front of the body midline, or the shoulder; the apparatus remained stationary. Participants could observe their hands in between test blocks.

Because this study was designed specifically to assess the effect of order of hand position on hand-specific orientation perception errors, I elected to use the "80° centred" method of generating the probe orientation on each trial (described in experiment 1 of this chapter). This method was shown to elicit some hand-specific errors while ensuring the probe appeared tilted inwards or outwards of the test orientation with equal likelihood.

Participants completed 4 blocks total in this experiment. Including set up and instruction, the experiment took roughly 45 minutes to complete. As per the previous experiment, myself or a junior research assistant was seated in the testing room throughout testing.

Data Analysis

Outlier analysis led to the removal of 24 pairs of accuracy and precision values. Of 1092 total pairs of values, 1068 were used in the analysis.

Accuracy values were analyzed in a mixed model linear regression, with the fixed effect of hand position order (midline first or shoulder first), hand (left or right), and test orientation (-30°, -20°, -10°, 0°, 10°, 20° or 30°). Degrees of freedom were corrected using the Sattherthwaite approximation [154]. All factorial interactions were tested. A second analysis was performed on precision values using the same parameters.

5.3.3 Results

Accuracy

Mean signed error for all conditions is shown in the top row of Figure 5.6.

There was a main effect of hand position order on signed error, $F(1, 34.90)=7.61$, $p=0.009$. There was also a main effect of hand, $F(1, 998.12)=7.89$, $p=0.005$, and a main effect of test orientation, $F(6, 998.40)=24.07$, $p<0.001$. There was a significant hand position order x test orientation interaction, $F(6, 998.40)=8.62$, $p<0.001$. No other main effects or interactions were significant. These results replicate the main effect of hand seen in the previous experiment. In addition they clearly show that the order in which participants complete position blocks leads to distinct changes in orientation judgment errors and the compression of perceived responses across the tested range.

Precision

Mean precision for all conditions is shown in the bottom row of Figure 5.6.

There was a main effect of hand on precision, $F(1, 36.70)=6.87$, $p=0.009$. No other effects or interactions were significant. Across all conditions, participants were less precise with their judgment of left hand orientation, compared to their right.

5.3.4 Experiment 2 Discussion

In this experiment, I compared two groups of participants, one group who completed the line matching task with the fingers in front of the midline, followed by the same task at the shoulder position, and a second group who completed the conditions in the reverse order. Consistent with previous work showing extended muscle contraction can lead to rotations of felt arm position in the direction opposite contraction [2, 141, 176, 180], I predicted that completing the midline rotation condition (which fatigued the bicep) first would lead to greater outward rotation of responses in the subsequent conditions, compared to when the condition order was reversed. This was the case; the orientation estimates in the shoulder position were ro-

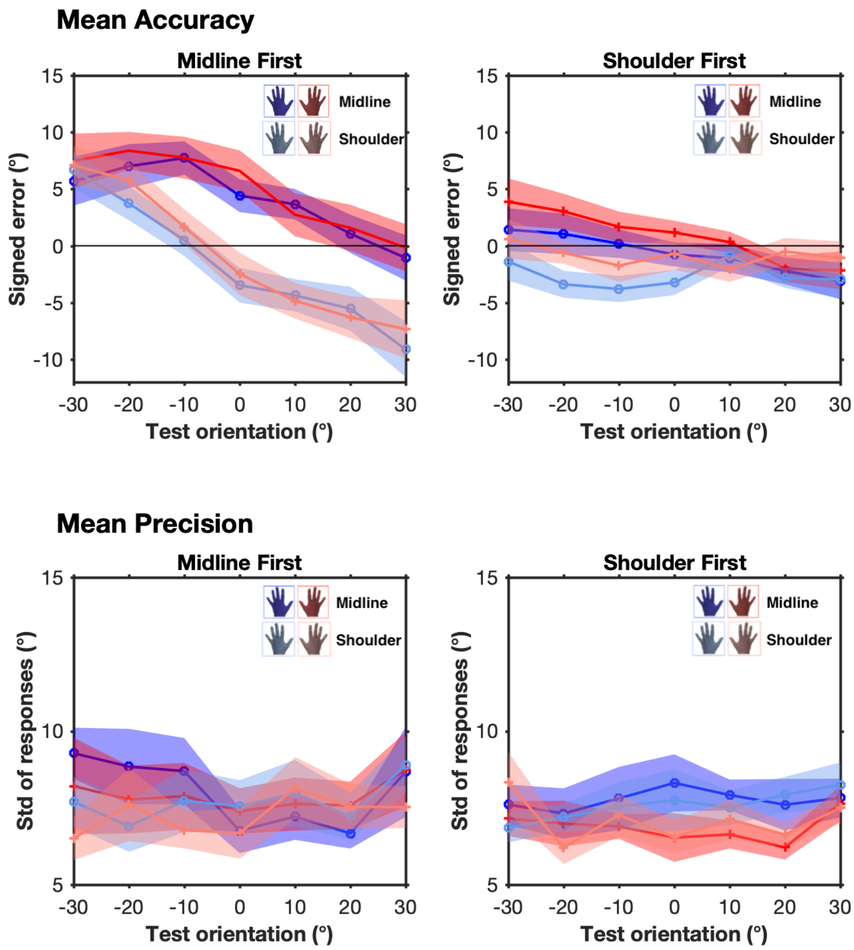

Figure 5.6: Top row: Mean signed error for the four hand x position conditions, for both hand position order types. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Bottom row: Mean precision of responses. Shaded error bars are standard error of the mean.

tated outward, in some cases upwards of 5°, when the midline condition was completed first, compared to the same test orientation when position order was reversed (see Figure 5.6). Additionally, I found that when the midline condition was completed first, there was a greater compression of responses across conditions, characterized by a steeper slope of signed error across the test range. This suggests initial discomfort or strain may have encouraged participants to make more conservative estimates of finger orientation throughout the experiment.

On average, right hand orientation estimates were biased more inwards than left hand estimates. This is consistent with what I observed in the previous experiment in this chapter. That is, with a balanced range of initial line orientations (e.g., equally likely to require being rotated inward or outward to match the test orientation), the asymmetry I observed in the previous Chapters (left hand rotated inward of right) is reversed (right hand rotated inward of left). Again in these studies, an experimenter was present in the room while participants completed the task, and this may have inadvertently led to different strategies of response compared to experiments in previous chapters, where there was no experimenter present in the room. More data is needed to support this possibility.

These data serve as a cautionary note for the use of within-subjects studies for limb and digit localization, or orientation estimation. The previous positions of the arm can create muscle strain and fatigue which subsequently influences response, and arm discomfort itself may be a confounding factor in terms of the strategies participants adopt when responding. While between-subjects methods may introduce individual differences that can obscure the effect of experimental manipulation, they avoid the effect of conditioning of muscles across conditions. Of course, future studies could also consider recording muscle activity during experimental trials, and correlating the degree of strain with deviations in subsequent responses, to determine whether repetitions of trials within conditions might still be a confounding factor.

5.4 Chapter Discussion

In this chapter, I described two control experiments which explored the impact of the test paradigm on participants' responses. In Experiment 1, I examined how the distribution from which the initial display line was sampled changed responses. I compared two uneven, uniform distributions (-15° to 30°; -40° to 40°), one even uniform distribution (80° range centred on the correct response) and a normal distribution with a mean of the correct response and a standard deviation of 10°. I found that the first of these distributions created a great deal of compression across the range of responses. This finding suggests that the compression in the data I observed in previous chapters was driven by the constrained, unbalanced sampling distribution of the initial line orientation. By contrast, wider distributions produced less compression. The uniform distributions all showed an asymmetry in responses, where participants judged the right finger as being more rotated inwards than the left (in contrast to previous chapters, which showed the opposite). The condition using a normally distributed distribution did not show a clear hand effect, but did produce the fastest response times. These data highlight the need for balanced sampling distributions for initial probe displays and careful consideration of display parameters.

In Experiment 2, I revisited the experiment described in Chapter 4 where I varied the position of the hand relative to the body midline. I used a balanced line orientation sampling technique that still showed evidence of asymmetry between the hands (the 80° centred). I was specifically interested in whether muscle strain and fatigue elicited by the "midline" condition might affect performance in the following block, compared to when the first block was the more comfortable "shoulder" condition. Completing the midline condition first led to more compression of responses, possibly reflecting more conservative responses when participants were strained or fatigued. I also observed that the condition following the midline block showed more outward rotational errors than its counterpart in the reversed-order group, consistent with the possibility that fatiguing the bicep in the previous block led to a drift of position estimates in the direction opposite contraction.

The findings described in this chapter illustrate the need for carefully designed experiments that maintain a consistent level of comfort across conditions. In addition, muscle activity and specifically muscle conditioning, may be a key factor in final digit position and orientation estimates. Future studies should consider the tradeoffs of a balanced uniform sampling method for display probes (longer response time, hand asymmetries) and sampling from a normal distribution (faster response times, no clear asymmetries). As well, recording muscle activity on a trial-by-trial basis may help elucidate the role of previous muscle strain on subsequent digit localization and orientation estimation. Presently, these results suggest a conservative interpretation of the results reported in previous chapters, as some of those findings may have been impacted by the nature of the experimental paradigm itself.

6 Perceived orientation of different fingers on the hand

6.1 Introduction

The studies reported in previous sections in this dissertation have focused specifically on orientation judgments of the index finger. Errors in these judgements hint at the potential character of proprioceptive maps of the finger, but it remains to be seen whether these errors can be generalized to other fingers, or even the entire hand. If rotational errors reflect a global rotation of the hand, one might expect that underlying representation to look something like the overlay in Figure 6.1A, where the rest of the fingers and palm are similarly tilted.

Alternatively, it may be that these errors reflect underlying distortions of the shape of the hand itself. Participants consistently misreport the dimensions of their own hands in hand shape perception tasks like the one described by Longo and Haggard [103]. In this task participants indicate the location of landmarks on their obscured hand using a pointer (this task is almost always performed on the left hand only, on the grounds that the right hand is more accurate in pointing) [103]. The authors claim that individuals have different, distorted topographical maps of the dorsal and ventral surfaces of the left hand [104]. Characteristics of the distortions of the ventral surface of the hand includes a widening of the palm and shortening of the fingers compared to veridical [103, 104, 106]; the magnitude of these distortions appears to change as a result of several factors such as hand posture (fingers spread or together) [100], the presence of uninformative vision (participants blindfolded or not) [99] and even task instructions (verbal or tactile cueing of landmarks) [121]. To my knowledge a comparison of distortions of the left and right hands has not yet been done.

If it were the case that the underlying representation of the (left) hand and fingers were consistently distorted, one might expect this to have a measurable impact on left finger orientation perception. That is, if the hand were judged as broader than actual, it could lead to a representation of the hand such as the one in Figure 6.1B. Such a distortion would predict consistent inward rotations of index finger orientation judgments (as observed in Chapters 3 and 4), and different, potentially opposite errors across other fingers on the hand. Of course, given the differences between the finger orientation judgment task and the landmark pointing task, it is possible that topographical distortions of the hand elicited by the present set of experiments may be quite different than those described by Longo and colleagues [99, 100, 103, 104, 106, 121]. Nevertheless, a difference between orientation judgment errors for different fingers on the same hand would support a theory of a distorted topographical representation of the hand, vs. a rotated representation with accurate topography.

In the present study, I tested perceived orientation of the index and ring fingers of the right and left hands at varying orientations around straight ahead. The index finger was chosen for comparison with my previous research; the ring was chosen for its relatively similar length to the index finger in most individuals. I was specifically interested in whether ring finger orientation errors would be consistent with index finger orientation errors, or substantially different. The former finding would suggest the errors in finger orientation perception that I have documented might be driven by a rotational error in whole hand representation; the latter would indicate orientation errors may stem from a distorted internal representation of the topography of the hand.

6.2 Methods

6.2.1 Participants

Nineteen female participants completed this experiment. Males were not intentionally excluded, but a convenience method of sampling led to only female participants in this study. Participant age ranged from 17-24 with a mean of 19 years $\pm$ 2. Participants all scored between 55 and 100 on the Edinburgh Handedness Inventory [22, 132], indicating they were all right handed. The mean EHI score was 89 $\pm$ 15.

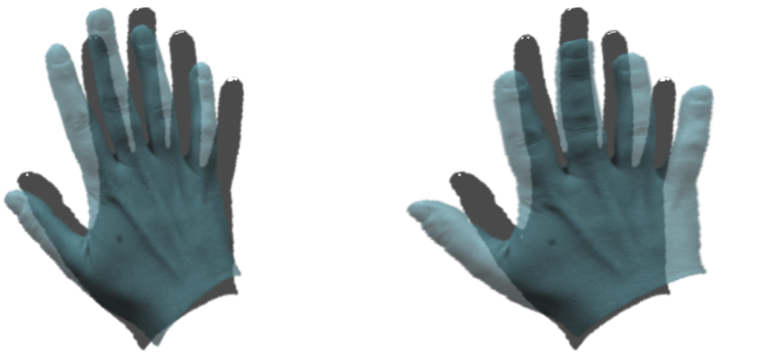

Figure 6.1: Two possibilities ways in which perceived finger orientations might represented: A) the hand is represented with accurate dimensions and relative positions, but the entire hand's orientation is misjudged, or B) if the hand's dimensions are distorted and this leads to unique errors in each fingers' perceived orientation.

6.2.2 Apparatus

The test apparatus was used in configuration B - "Horizontal" for this experiment (see Figure 2.1).

6.2.3 Procedure

Seven test orientations were used: -30° to 30° in 10° steps. Each test orientation was repeated 8 times in a block and within-block trial order was randomly shuffled.

Trials proceeded as described in the General Methods. All participants completed blocks with the left and right hands, with either the index or ring finger attached to the rod (see Figure 6.2). There were four blocks total, one for each hand x finger combination. The order in blocks were tested was randomized. Participants could observe their hands in between test blocks.

I used the "Normally Distributed" method of generating the probe orientation on each trial (described in Chapter 5 Experiment 1). This method reduces hand-specific errors while ensuring the probe appears tilted inwards or outwards of the test orientation with equal likelihood.

Participants completed 4 blocks total in this experiment. Including set up and instruction, the experiment took roughly 45 minutes to complete. Either myself or a junior research assistant sat with participants in the testing room during the experiment.

Figure 6.2: Images of the two fingers as they were attached to the rod.

6.2.4 Data Analysis

Outlier analysis led to the removal of 22 pairs of accuracy and precision values. Of 532 total pairs of values, 510 were used in the analysis. Outlying data were from 5 individuals: 3 people (index), 1 person (ring) and 1 person (index and ring).

Accuracy values were analyzed in a mixed model linear regression, with fixed effects of finger (index or ring), hand (left or right), and test orientation (-30°, -20°, -10°, 0°, 10°, 20° or 30°), with intercepts as a random effect. Degrees of freedom were corrected using the Sattherthwaite approximation [154]. All factorial interactions were tested. A second analysis was performed on precision values using the same parameters.

6.3 Results

6.3.1 Accuracy

Mean signed error for all conditions is shown in the top row of Figure 6.3.

My analysis did not find any main effects or interactions on signed error.

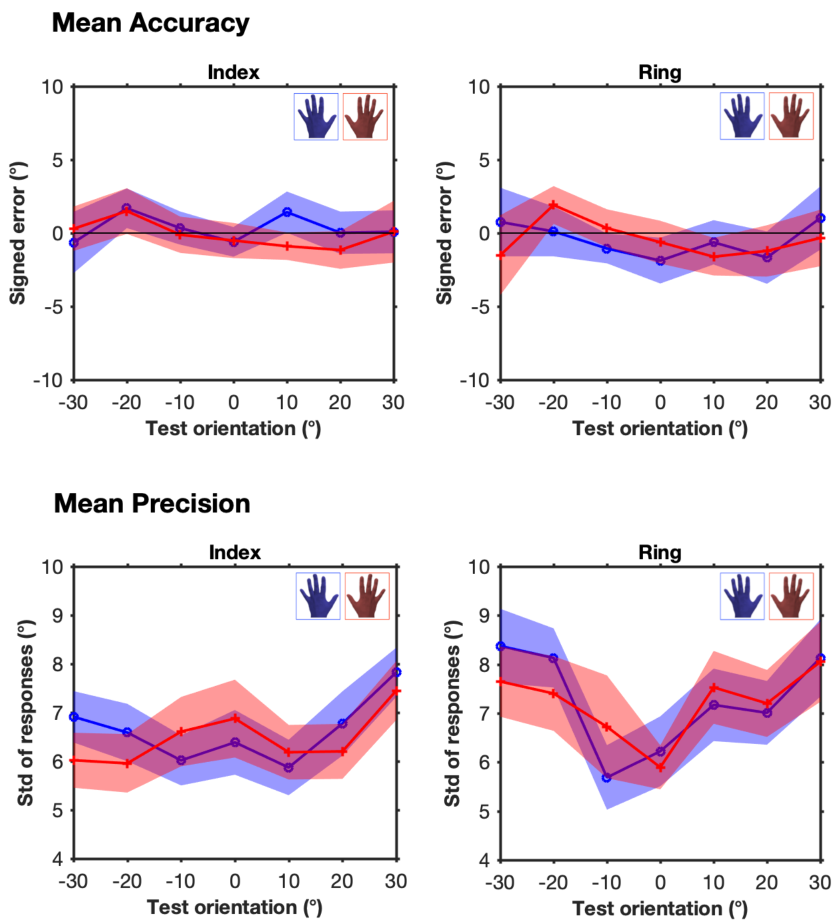

Figure 6.3: Top row: Mean signed error for the four finger x hand conditions. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Bottom row: Mean precision for the four finger x hand conditions. Shaded error bars are standard error of the mean.

6.3.2 Precision

Mean precision for all conditions is shown in the bottom row of Figure 6.3.

There was a main effect of finger on precision, $F(1, 463.70)=13.39$, $p<0.001$. There was also a main effect of test orientation, $F(6, 463.56)=4.20$, $p<0.001$. No other main effects or interactions were significant. Results indicate that precision was worse for the ring finger than the index finger. Precision was also worse for more extreme test angles compared to angles in the middle of the test range (see bottom row of Figure 6.3).

6.4 Discussion

This chapter describes a single experiment in which I compared orientation perception of the index and ring fingers on both left and right hands. I had posited that a difference in accuracy between fingers would be evidence for a distortion of the participants' underlying representation of their hand's shape and dimensions. In contrast, failure to find such differences would be consistent with the possibility that the proprioceptive representation of the hand is topographically accurate, but rotated. While I did find participants were more variable in their orientation judgments of the ring finger (unsurprising, given the unfamiliarity of such a task), I failed to find any significant difference between hands or fingers in orientation judgment errors. In fact, in Figure 6.3 it is evident that participants' accuracy was quite high overall. While a failure to find an effect must be interpreted carefully, my results in this experiment are consistent with an accurate representation of the hand and its orientation.

These results are a contrast to the highly repeatable and measurable localization errors found in the landmark pointing task [99,100,103,104,106,121], which have been cited as evidence for a distorted body schema underlying hand and finger perception. My data do not indicate that a similar schema is invoked for my orientation judgment task. As discussed in Chapter 1, there is considerable debate over how many body maps are used by the brain and under what circumstances. It is an open question whether some of those maps might contain topographical distortions while others are more accurate [28, 77]. It may be the case the the landmark pointing task relies more on a visual or semantic representation of the hands to determine the location of knuckles, fingertips, etc., whereas such representations may be less relevant for orientation perception. A difference in the weighting of top-down contributions to these two tasks may explain some of the inconsistencies in the kinds of errors observed between tasks [28].

Chapter 5 illustrated that simple methodological differences, even within the same kind of task, can lead to substantive changes in participants' performance. In this chapter, I sampled the original orientation of the probe line from a normal distribution, and found that both ring and index finger orientation was on average accurate, in contrast to several of the previous studies in this dissertation. It seems clear that hand and finger perception are highly influenced by the task used to probe them. The next and final experimental chapter in this dissertation also uses the normal distribution method of sampling, and provides evidence that differences in hand posture still play a critical role in the accuracy of finger orientation perception.

7 Hand posture influences perceived finger orientation

7.1 Introduction

So far, I have restricted my analysis of perceived finger orientation to when the palms are facing out (Chapter 3) or down (Chapters 3–6). An outstanding question is whether finger orientation perception is modulated by changes in the posture of the hand (e.g., pronated or supinated). Longo and Haggard report that landmark pointing tasks, like those described in the previous chapter, find similar localization errors for the palm and the back of the hand, but these errors vary in their magnitude, with the palm of the hand being localized more accurately [104]. The authors concluded that internal maps of the two surfaces may not be equivalent. This change in magnitude of error is not seen when the hand is simply rotated, palm-down, to 90° so that the thumb points towards the midline [103] suggesting differences in localization ability are unique to hand surface, not rotational position.

Mancini and colleagues tested localization of touches delivered to the palm and the back of the hand, and found evidence that touches on the palm were localized more accurately. Similar to the landmark localization task described above, rotating the hand 90° did not impact localization of touches on the back of the hand [113]. Interestingly, observed errors were consistent across tactile, nociceptive and thermal stimulation, suggesting that localization errors did not reflect properties of afferent nerve fibres. The authors instead suggest that these errors reflect distortions of the underlying perceptual map of the hands [113].

Why might the palm of the hand be mapped more accurately than the back of the hand? Mancini and colleagues observed a general trend that touches applied to more densely innervated skin were localized more accurately [113]. This is consistent with a top-down influence of a more accurate internal hand map; that is, more precise tactile processing over time may help build up a more veridical representation of the surface of the hand in the brain.

It's unclear whether this localization advantage for the palm of the hand extends to position and orientation sense. That is, is it easier to estimate the position and orientation of the ventral surface of the finger, compared to the dorsal surface? To my knowledge, no study has tested arm or hand position sense between a palm-up and a palm-down posture in the same plane and paradigm. This is a major oversight, as it determines the generalizability of findings of hand and limb position sense research. Comparisons of hand postures across studies are difficult: as I demonstrated in Chapter 5, methodological differences in the testing paradigm may have substantial effects on performance. Therefore, in the current study I directly tested whether finger orientation perception is modulated by what surface of the finger is facing upwards in the task. I had participants complete a version of my line-matching task with the palm oriented up, or down (see Figure 7.1). To account for potential fatigue or muscle conditioning influencing results, I conducted both a within-subjects and a between-subjects version of this experiment. The two versions are described side-by-side in the methods and analysis, for ease of comparison.

Consistent with evidence that the palm of the hand may be more accurately localized than the back of the hand [103, 104], I predicted that I would observe more accurate, precise performance when localizing the fingers with the palms facing up, compared to palms facing down. Consistent with the findings of Chapter 6, I did not anticipate differences in performance between the left and right hands.

7.2 Methods

Participants

Participant demographic information is shown in Table 7.1. The participants are divided into the "within-subjects" group, who completed all posture conditions, and the "between-subjects" group, with individuals who completed only one of the posture conditions and were compared to one another in a separate analysis.

Group	n (f, m)	Age: Range (years)	Age: Mean (years)	EHI Score: Range	EHI Score: Mean
Within-subjects	29 (20, 9)	17–33	22 ± 3	55–100	90 ± 13
Between-subjects	32 (22, 10)	18–34	20 ± 3	50–100	85 ± 16

Table 7.1: Participant demographics for Chapter 7

Apparatus

The test apparatus was used in configuration B - ”Horizontal” for this experiment (see Figure 2.1).

Procedure

Seven test orientations were used: -30° to 30° in 10° steps. Each test orientation was repeated 8 times in a block and within-block trial order was randomly shuffled.

Trials proceeded as described in the General Methods. I was interested in isolating the effect of hand posture on finger orientation perception. As such I wished to minimize other influences on orientation errors. Therefore we used the ”Normally Distributed” method of generating the probe orientation on each trial (described in Chapter 5 Experiment 1). This method reduces hand-specific errors while ensuring the probe appears tilted inwards or outwards of the test orientation with equal likelihood.

In all conditions the hand was positioned directly in front of the shoulder. There were four possible experimental blocks, with the left and right hands either 1) palm up or 2) palm down (see Figure 7.1).

Within-subjects. The within-subjects group completed all four experimental blocks. The order in which the hands were tested was counterbalanced across participants. Including set up and instruction, the experiment took roughly 45 minutes to complete.

Between-subjects. The between-subjects group were randomly assigned to either ”palm up” or ”palm down” and completed the task for both the left and right hands in this posture. Due to scheduling problems, seventeen participants completed the palm down condition and fifteen completed the palm up condition. Order of the hands tested was randomized. Including set up and instruction, the experiment took roughly 30 minutes to complete.

As with previous experiments, participants could observe their hands in between test blocks. Care was taken to ensure participants were comfortable in all tested conditions: an adjustable elbow cushion was provided. Either myself or a research assistant was present in the testing room while the experiment took place.

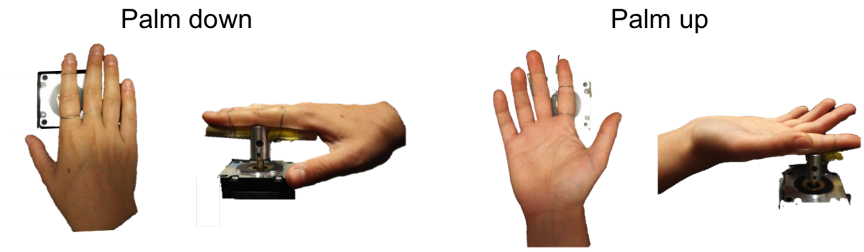

Figure 7.1: Images of the hands in the palm down and palm up postures.

Data Analysis

Data for the within-subjects and between-subjects groups were analyzed separately.

Within-subjects. Outlier analysis led to the removal of 30 pairs of accuracy and precision values. Of 812 total pairs of values, 782 were used in the analysis.

Between-subjects. Outlier analysis led to the removal of 9 pairs of accuracy and precision values. Of 448 total pairs of values, 439 were used in the analysis.

Accuracy values were analyzed in a mixed model linear regression, with the fixed effects of hand posture (palm up or palm down), hand (left or right), and test orientation (-30°, -20°, -10°, 0°, 10°, 20° or 30°). Intercepts were treated as a random effect. Degrees of freedom were corrected using the Sattherthwaite approximation [154]. All factorial interactions were tested. A second analysis was performed on precision values using the same parameters.

7.3 Results

Accuracy

Mean signed error for all conditions is shown in the top row of Figure 7.2.

Within-subjects. There was a main effect of hand posture on signed error, $F(1, 726.64)=267.15$, $p<0.001$. There was also a main effect of test orientation, $F(6, 726.39)=14.40$, $p<0.001$. There was also a significant posture x hand interaction, $F(1, 726.67)=6.39$, $p=0.012$. No other effects or interactions were significant. A follow up comparison found that signed error was significantly different for the left and right hands in the palm down posture, $F(1, 726.79)=8.27$, $p=0.004$, but not in the palm up posture ($p=0.49$). Results indicated that when the palm is facing up, all responses deviate inwards towards the body midline; when the palm is down responses are closer to accurate, but the left hand shows some outward rotation, similar to what was observed in Chapter 5. Additionally, the data showed that even with a normally distributed probe display, there was still some compression of responses across the test range.

Between-subjects. There was a main effect of hand posture on signed error, $F(1, 29.75)=57.71$, $p<0.001$. There was also a main effect of test orientation, $F(6, 381.37)=4.62$, $p<0.001$. There was also a significant posture x test orientation interaction, $F(6, 381.37)=2.27$, $p=0.036$. No other effects or interactions were significant. Follow-up analyses found that for each of the seven test orientations, there was a significant difference in hand posture, $p=0.012$ or less. Results replicated those in the within-subjects group, in that when the palm is facing up, responses deviate inwards towards the body midline. A main effect of hand was not observed.

Precision

Mean precision for all conditions is shown in the top row of Figure 7.3.

Within-subjects. There was a main effect of hand posture on precision, $F(1, 725.33)=69.50$, $p<0.001$. Precision was worse in the palm-up conditions. There was also a main effect of test orientation, $F(6, 725.19)=7.68$, $p<0.001$. No other effects or interactions were significant.

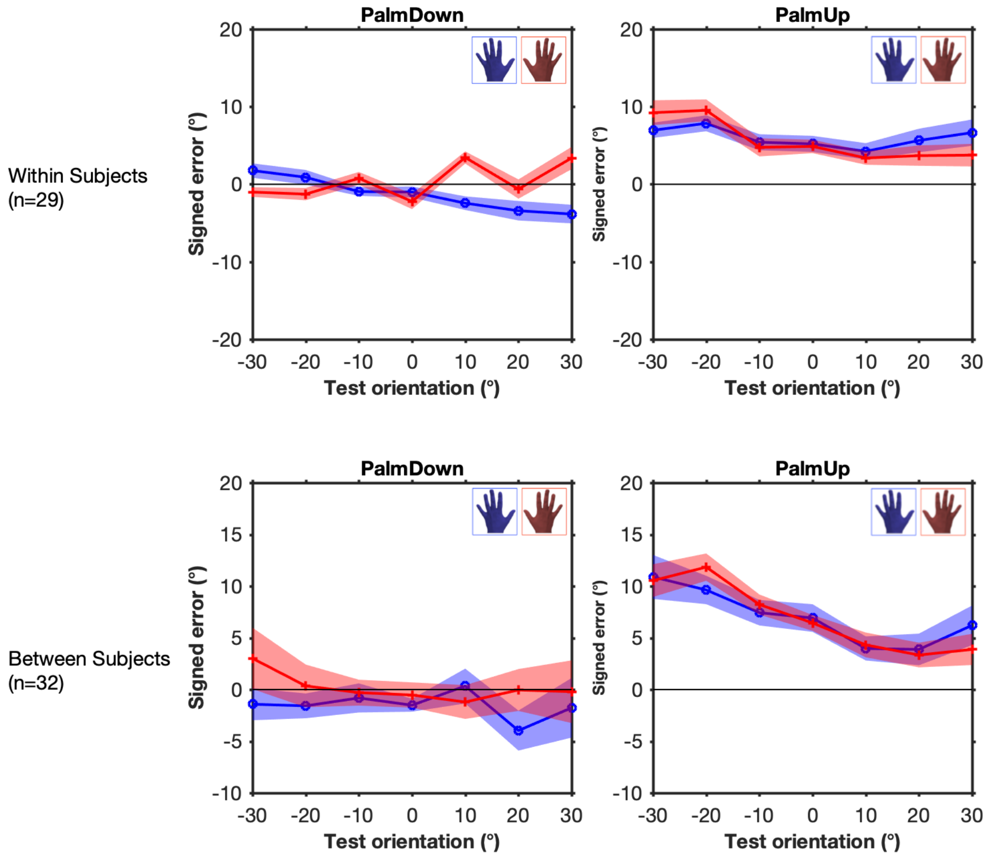

Figure 7.2: Top row: Mean signed error for the four hand x posture conditions for the within-subjects group. Positive values indicate an inward rotation from vertical; negative values are an outward rotation. Bottom row: Mean signed error for the four hand x posture conditions for the between-subjects group. Shaded error bars are standard error of the mean.

Between-subjects. There was a main effect of test orientation on precision, $F(6, 380.77)=3.72$, $p=0.001$. There was also a significant posture x hand interaction, $F(6, 380.70)=6.31$, $p=0.012$. No other effects or interactions were significant. Follow up analysis showed that precision for the left hand was significantly worse than the right hand in the palm up posture, $F(1, 38.43)=4.47$, $p=0.041$, but this was not the case for the palm down posture ($p=0.73$). To summarize, the palm up posture led to selective impairment in precision of responses for the left hand; precision varied with test orientation such that precision was worse for more extreme test angles.

Figure 7.4 shows precision collapsed across postures and hands, for both within-subject and between-subject groups. This figure illustrates the increase in response variability particularly for extreme inward rotations of the hand. Figure 7.4 further shows that precision was worse for the between-subject group compared to the within-subject group. These data suggest practice may play a role in reducing variability in responses. Nevertheless the pattern of increased variability at extreme inward angles remains clear.

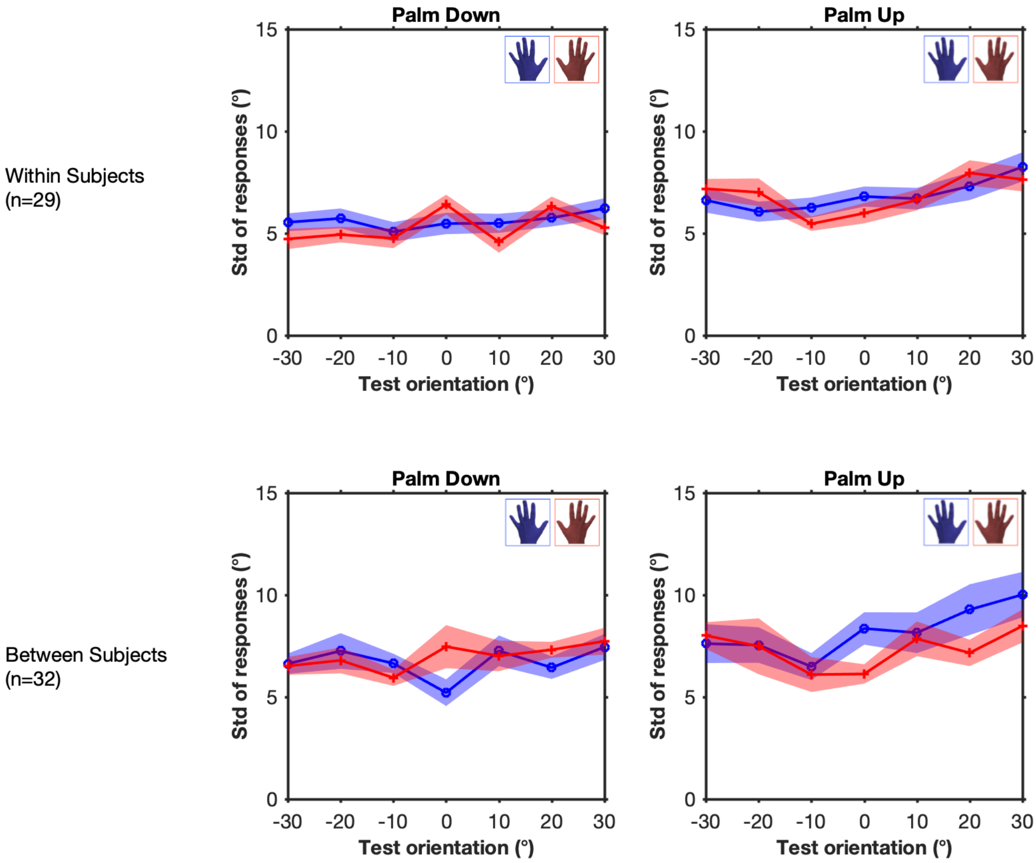

Figure 7.3: Top row: Mean precision for the four hand x posture conditions for the within-subjects group. Bottom row: Mean precision for the four hand x posture conditions for the between-subjects group. Shaded error bars are standard error of the mean.

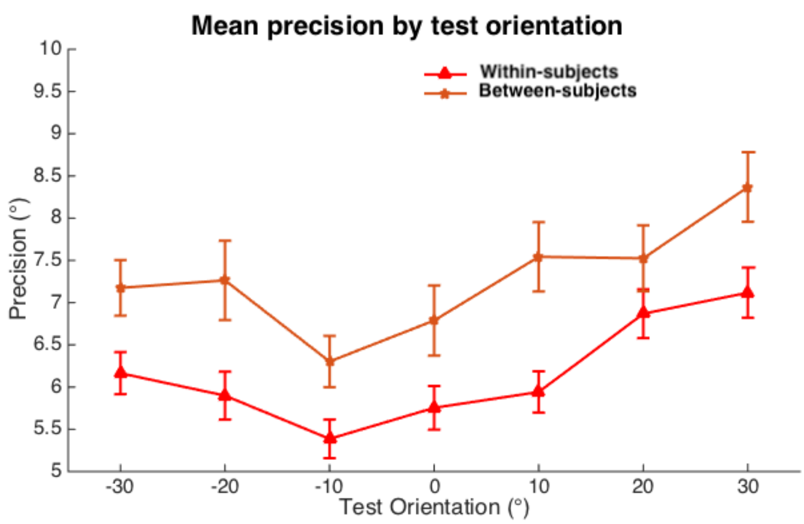

Figure 7.4: Mean precision collapsed across hands and postures for both groups. Error bars are standard error of the mean.

7.4 Discussion

In this chapter I examined the role of hand posture on finger orientation perception. Other studies have found that hand landmarks (e.g., the tip of the finger, the first knuckle) are localized more accurately on the palm of the hand, compared to the back of the hand [103, 104] Additionally, physical stimuli applied to the palm are localized more accurately than those applied to the back of the hand [113]. The authors of these studies have concluded that the internal body map of the palm is less distorted than the back of the hand, possibly due to increased innervation of the skin surface, and subsequent high-precision calibration of visual-tactile inputs.

In the present study, I sought to determine whether participants could more easily determine the orientation of their finger when the palm was facing upwards, compared to when it faced downwards. I compared finger orientation perception when the palms were facing up vs. facing down, using both within- and between-subjects experimental designs. Consistent with previous localization tasks I had predicted that finger orientation perception would be more accurate and precise when the palm was facing up. If this were the case, then it would indicate that a distorted internal body map may be used in finger orientation perception, as well as other forms of hand perception. In fact, I found the opposite of my predictions: in both variations of the study, finger orientation perception was biased substantially more inwards, up to almost 10° in some instances, when the palms were facing upwards compared to when they faced down. Additionally, the palm-up condition produced more variable responses in both hands for the within-subjects group, and for the left hand in the between-subjects group. Thus, I provide clear evidence that, contrary to other kind of localization paradigms, finger orientation perception is better when the palms are oriented downward. In contrast to my previous studies using uniform sampling distributions for the display line, I observed no difference in accuracy between the left and right hands in this task. This finding replicates those of Chapter 5 Experiment 1 and Chapter 6, both of which showed that sampling from a normal distribution of line orientations does not lead to an asymmetry between left and right finger perception.

In this experiment, I was careful to ensure that participants were comfortable in all tested conditions. Because I did not record muscle activity, I cannot rule out the possibility that there were different degrees of muscle strain in different conditions used in this task, and some of my findings may be the result of differential muscle conditioning and fatigue. In particular, strain of the muscles in the forearm, which extend to control flexion and extension of the fingers (e.g., extensor digitorum communis, extensor indicis, flexor digitorum profundus, and flexor digitorum superficialis [114]), may have varied across experimental conditions as a result of the rotation of the elbow joint. Targeted EMG recording could confirm this speculation, and is arguably a necessity in future experiments. Nevertheless, at the behavioural level these results confirm that perception of finger orientation is not consistent across postures of the hand.

As was the case in Chapter 6, my data here also do not agree with tactile and landmark localization tasks, which show an advantage for the palm over the back of the hand [103, 113]. This contrast provides further support for the possibility that tactile and semantic perception of the hands differs from perception of orientation. This may be the result of different body representations for different modes of perception, as I discussed in Chapter 1. That is, there are many representations of the body in the brain for different uses, such as for perception versus action [77]. Alternatively, taking the Bayesian approach proposed by De Vignemont [28], inconsistencies in the direction and magnitude of localization bias across paradigms could indicate a difference in the weighting of sensory contributions to the final percept queried by the paradigm (e.g., emphasizing *a priori* internal maps of the hand for landmark perception, over muscle strain and skin stretch for dynamic position sense). This experiment provides yet more data to indicate that finger and hand perception is highly context-sensitive. This is a topic I will return to in the next chapter.

An interesting and novel finding of this study was that the within-subjects group were more precise than the between-subjects group (see Figure 7.4). This finding runs counter to my earlier suggestion that fatigue may introduce imprecision over time; rather, these data suggest that, at least for relatively comfortable arm positions, practice with the task may improve precision of responses. There is some evidence that repeated experience with limb localization, as in dance training, may lead to improved proprioceptive position sense [75, 146], though whether this finding can be extended to perceived finger orientation remains unclear. Unfortunately, due to the low number of repetitions of each test orientation in a block, and the randomization of the order of test orientations, this study lacks the statistical power to compare precision of responses early and late in the test session. A future study could directly address the effects of practice on orientation perception by having participants complete multiple sessions using the line-matching task, to determine the long-term effects of practice on performance.

Other studies of hand and arm localization have used either a palm-up or a palm-down arm posture in their task. Despite testing a single hand posture, some of these authors (myself included) have generalized their findings to ”perceived hand position” (e.g., [1, 45, 46, 67, 144, 147]). The present experiment provides evidence that this generalization may be unfounded; rather, different hand postures result in differences in orientation perception, and potentially localization as well. These results could be interpreted as a bias induced by an *a priori* body representation, which is distorted by varying amounts for different surfaces of the body. If this were the case then we would need to stipulate the existence of several body representations in order to explain inconsistent ”distortions” across different orientation estimation and stimuli/landmark localization tasks [77, 103, 113]. These results might be more simply explained by differences in the biases in proprioceptive signals produced by different postures, a possibility which merits further exploration. Nevertheless, these data serve as a cautionary note that grand statements about limb and digit localization must be thoroughly tested to confirm their claims hold across different postures.

8 Discussion

The aim of this dissertation was to identify some of the contributing factors to perceived finger orientation, specifically in the absence of vision. Understanding these contributions can inform the development of more comprehensive theories (and more tightly controlled experiments) regarding limb and body position sense. No work has examined the perceived orientation of the fingers, which is a fundamental component of perceived limb position. There are a number of methodologies for testing hand and arm position sense, but the use of pointing and joint positioning techniques introduce the confound of whether the position sense of the other limb can interfere with response. I elected to use a paradigm in which participants adjusted a visual line to match the orientation of their passively moved, unseen finger, in order to measure the accuracy and precision of finger orientation sense.

8.1 Perceived finger orientation is context-dependent

Factors which significantly influence perceived finger orientation include: whether vestibular processing is disrupted, whether the probe used to judge orientation is visual or non-visual, and which hand is used (Ch 3), participant handedness (Ch 4), display parameters and possible muscle conditioning (Ch 5), and participant hand posture (Ch 7). This list is certainly not exhaustive, and there are likely many other parameters which affect finger orientation perception.

Perceived arm and hand position is also sensitive to changes in context. At least one study has reported individual differences in arm position sense that are consistent across time [147]. Specific forms of training, such as dance, may improve position sense [75, 146], potentially giving rise to some of these differences across participants. More recent experience can also alter position sense; adapting participants to a specific manual workspace can lead to a drift towards that workspace in subsequent limb localization tasks (however, the authors did not account for the potential contributions of muscle conditioning in that study) [52]. Perceived position of even a static limb has been shown to drift over time [15, 177]. Although a number of authors have pointed to a stable, distorted underlying representation of the body that leads to errors in landmark and tactile localization [99–106, 113, 126], simple manipulations like flipping the hands over or splaying the fingers lead to differences in the types of localization errors observed [100, 104], raising questions of how stable these underlying representations truly are. Finally, differences in performance on matching arm positions to visual vs. proprioceptive targets hints at different strategies for localization depending on the nature of the probe [57,58,170]. Taken together, these data imply a complex and dynamic system for limb and digit perception.

This complexity unfortunately makes generalizations across different research paradigms difficult. Critically, a model of upper limb perception must be able to address the contexts in which perception is altered, and when it is robust. De Vignemont's Bayesian model of the body image and schema is instructive [28]. In this model, the distinction between different kinds of internal body models is a matter of the relative weighting of different sensory and top-down inputs. Dynamic orientation and position sense may be similarly constructed, with many weighted inputs integrated in some optimal fashion to create a final internal estimate. The question is then which inputs matter, and how context might directly alter these inputs or the weighting assigned to them by our perceptual systems.

8.2 Perceptual responses depend on the response methodology

A specific context to which finger orientation estimates are sensitive is the type of response methodology. This includes the nature of the probe participants are comparing orientation estimates to (visual or non-visual, Ch 3) and how probes are likely to appear (lines with different sampling distributions for their initial orientation, Ch. 5). I am not presuming that these factors influence finger orientation perception itself; however, they do seem to influence how participants respond. This finding highlights the need for comprehensive test batteries when examining complex percepts such as body and limb position sense. Other methods, such as forced-choice discrimination paradigms, may be a useful complement to existing methods. Similarities and differences in the observed response errors across test paradigms may provide insight into the origin of these errors (e.g., inaccurate visualization of the finger, strain in certain arm poses, recruitment of semantic maps of the body, etc.). More data are needed to parcel out effects driven by the testing protocol and effects that truly represent orientation sense.

8.3 Perceived finger orientation may be influenced by muscle conditioning and fatigue

In Chapter 4, I showed that perceived orientation of the fingers appeared to deviate outwards as the hands were positioned further from the body midline. This is consistent with measures of haptically-perceived parallel, which also deviates outward with more lateral hand positions. Deviations in haptically-perceived parallel have been taken as an indication that haptic space is not Euclidean [79–82, 153, 184]. However, a control experiment in Chapter 5 provided evidence that the observed effect may be the result of muscle conditioning and fatigue. More research, which specifically targets and measures the role of muscle activity in these tasks, is needed to confirm this possibility. My data are consistent with evidence from other limb localization tasks that show prolonged muscle contraction and fatigue can lead to a drift of perceived limb position in the direction opposite contraction [2, 176, 180]. This reflects the thixotropic properties of muscles that lead to changes in background muscle spindle firing rate when the muscle is tensed and relaxed without changing its length [141]. I also did not control for the stretch of skin around the joints in my task. Skin stretching has been shown to contribute to position sense [35, 140]. These data emphasize that proprioceptive inputs must be carefully monitored and controlled in limb position perception experiments, as they can inadvertently influence position and orientation estimates. A comprehensive model of limb perception absolutely must take into account the constant contribution of these factors.

8.4 Perceived finger orientation is a function of hand posture

In Chapter 7, I demonstrated that using a carefully controlled line display, perceived orientation of the fingers deviates significantly inwards towards the body midline when the hands are supinated (palm facing up), versus when they are pronated (palm facing down). This result was shown for both a within-subjects group and between-subjects group. These findings are inconsistent with the literature on tactile and hand landmark localization, which finds the palm is perceived more accurately than the back of the hand. The authors of those studies have suggested that the internal representation of the palm of the hand may be less distorted [103, 113]. While this may be true for certain kinds of perceptual tasks, for perception of the orientation of the fingers it seems that perception is more accurate when the palms are facing down.

Importantly, the differences in orientation perception across hand postures raises a critical point about the generalizability of findings across hand and finger perception experiments. That is, my findings here suggest that the results of a finger or hand localization experiment conducted with the hand pronated, may not hold when the hand is supine. Future studies should consider testing localization and orientation perception in a variety of hand postures to inform the scope of their conclusions. Additionally, care should be taken in making inferences about the nature of static, long-term internal maps of the body, based on errors that are only found in certain tasks or postures.

This lack of generalizability across hand postures may be due to differences in internal representations of different surfaces of the hands, as some have suggested [103, 113], although it could indicate different representations are used for tactile and landmark localization versus orientation perception. Alternatively, it may be the case that the muscles associated with supination of the arm provide inaccurate position signals. Supination of the forearm is controlled by the supinator muscle of the forearm and the biceps brachii of the upper arm, both of which work against pronator muscles to rotate the radius of the forearm so that it lies parallel with the ulna [94]. If either of these muscles provides inaccurate position sense (or if they are easily fatigued) this might translate to rotational errors in perceived finger and hand position over time. Applying vibration to these muscle groups, or conditioning them, and measuring subsequent localization/orientation perception, may yield interesting insights into the role these muscles play in signalling hand and arm position. The possibility of inaccurate proprioceptive afferent signals must be ruled out before claiming that rotational errors represent higher-order biases in body representation(s).

8.5 Perceived finger orientation is altered by vestibular noise

In Chapter 3, I observed that applying disruptive galvanic vestibular stimulation (dGVS) causes inward rotational errors in finger orientation perception. This finding must be replicated with other display parameters (see Chapter 5). However, if this effect proves to be a general consequence of dGVS on finger orientation perception, this would implicate the vestibular sense in the perception of limb and digit position. Considerably more work needs to be done in this area to arrive at a comprehensive understanding of the role of vestibular inputs for position sense. In particular, the aftereffects and decay period of dGVS are not well understood, and within-subjects experimental designs must be cautious of GVS-related effects corrupting their control conditions.

Despite this gap in our current understanding of the effects of dGVS, I offer some tentative speculation about the possible role of vestibular inputs in finger orientation perception. This speculation is based on an observation I made in Chapter 3, that dGVS affected perceived finger orientation in the visual line-matching task, but not in non-visual tasks (e.g., comparing finger orientation to gravitational vertical or straight ahead). This would seem to implicate the vestibular system specifically in the direct comparison of a visual signal with a proprioceptive position signal. Evidence suggests that directional GVS can lead to rotational deviations in drawings made with an unseen hand [65]. It also impairs performance on a task in which participants must imagine themselves in a scene and point out directions from this imagined perspective [32]. Critically, in these affected tasks the position of the body and limbs is either unseen or must be inferred, and must further be compared to a visual coordinate system. A clever study of the effects of GVS on mental rotation of images by Lenggenhager and colleagues found that GVS only impaired performance in participants who reported mentally rotating their own imagined perspective to complete the task, and did not affect those who reported mentally rotating the image itself [92]. Thus, vestibular disruption may not directly influence non-visually perceived position sense, but may instead disrupt integration of felt or inferred position signals with visuospatial processing. It has been suggested this disruption reflects interference of the vestibular signal in temporo-parietal regions of the brain where this integration likely takes place [32]. If true, this would imply that comparison of perceived limb positions with non-visual targets, as in Chapter 3, is performed in other regions of the brain. Targeted fMRI studies could confirm this hypothesis.

8.6 Do we need an internal body map, or a default body position, to estimate finger orientation?

There is general consensus that the brain implements several high-level representations of the body for both perception and action. At least two distinct representations have been proposed, one for visual body characteristics and one for action-based mapping [28, 29, 71, 76, 77]. A third map of semantic relations of the body has also been suggested, which might include high-level associations such as the role of specific body parts [133]. These maps must contain some understanding of the dimensions (i.e., length and width) of the limbs, as this information is not provided by online proprioceptive inputs. Some authors have proposed that internal body maps may also contain default or canonical position information [71], and some evidence from studies on crossed limbs and ownership illusions supports this possibility [7, 168]. A number of authors have suggested internal body maps may be highly distorted; specific distortions have been proposed based on observed errors in body landmark localization and touch localization [99–106, 113, 121, 126].

However, other kinds of proprioceptive localization tasks do not necessarily generate errors consistent with these proposed distortions [147]. This lack of generalizability raises a question about how many internal body maps might exist, and under what circumstances they are used.

In earlier interpretations of my data, I had proposed that the asymmetries across hands in the control conditions of Chapter 3, and in Chapter 4, might reflect a bias in right-handers towards common functional poses of the hands [45, 46]. However, in subsequent studies I did not replicate this asymmetry, and further showed that compression of responses towards specific orientations were not consistent across different sampling distributions of the initial probe line orientation (Chapters 5 and 6) or hand postures (Chapter 7). Taken together, the experiments in this dissertation do not suggest a single consistent or canonical position underlying finger orientation perception. Rather, my results suggest a more dynamic perceptual mechanism, which is highly sensitive to variations in experimental paradigm and afferent sensory inputs.

Of course, finger orientation perception must still utilize some top-down assumptions regarding limb and finger length, as this information is not provided by afferent signals and is necessary to arrive at final position and orientation estimates. However, I did not find compelling evidence to suggest these assumptions are distorted or biased in a consistent fashion. My data instead suggest that bias may come from different response strategies, and possibly muscle fatigue, though these theories need to be explored further. I would venture to claim that these particular features must be critically assessed in all experiments that make inferences about distortions of internal body maps, particularly as a means of explaining errors in dynamic position sense.

8.7 Directions for future research

This research has raised a number of new questions which must be addressed in order to form a clear picture of how finger orientation is estimated and maintained. In addition to the gaps I have highlighted in my previous chapters, there are also major questions that I was unable to address in the scope of my dissertation, which would contribute a great deal to a final comprehensive model of limb and digit position sense. In this section, I discuss some of these research questions and how they might be addressed in future experiments. In all future experiments, I recommend recording muscle activity in the upper arm and forearm using electromyography or other methods, in order to directly correlate muscle activity with biases and variability in the perceived orientation of the fingers. Additionally, it would be useful to probe participants' confidence in their responses, perhaps by asking them to give some kind of percentage rating after each trial. This, along with interview questions following the experiment, may help shed light on participants' response strategies and how they might impact performance.

8.7.1 The drift of perceived finger orientation over time

A number of studies have shown that perceived limb position drifts over time, particularly following repeated unseen arm movements [15, 177]. In Chapters 4 and 5, I found that different hand positions can lead to rotational errors in finger orientation perception. Though more direct experimental evidence is needed, my results hint that muscle fatigue may play a role in the drift of finger perception over time. An outstanding question is how finger orientation perception changes over time in the absence of muscle strain. Wann and Ibrahim measured proprioceptive drift of an unmoving arm when it was visually occluded for up to 2 minutes, and found a drift of localization estimates towards the body. The authors indicate that the arm was supported by two arm rests, but do not mention whether the palm was facing down or up in the task (though from their simplified figures it appeared to be palm up). This drift of hand localization was reduced, but not completely resolved, by brief visual images of the limb's position, or proprioceptive stimulation akin to minor limb adjustment [177]. The authors also found that directing participants to attend to their limb position produced larger localization errors than when participants were distracted by a secondary task [177]. They posited that the observed drift of perceived limb location reflected a down-weighting of proprioceptive signals as they decayed over time, and subsequent larger emphasis on a more visual map of the limbs. Why this visual map contained inaccurate position information was not explored [177].

Jeannerod has suggested that proprioceptive information must constantly be recalibrated by visual feedback, and in the absence of this feedback localization may drift [74]. A number of my experiments, in particular Chapters 6 and 7, do not support the notion of a drifted representation of the fingers, though as I noted in the introduction different localization tasks can produce varied results, calling into question whether the drift reported in other studies represents a general mechanism or a specific case. However, my task included a great deal of intermittent proprioceptive feedback as the hand was passively rotated around, and this may have mitigated a certain amount of drift [177]. Therefore, a future study should examine how perceived finger orientation drifts as a function of longer durations without movement. This could be combined with manipulations of muscle strain to examine the interplay between muscle conditioning and fatigue and the simple passage of time, and their role in finger orientation perception.

8.7.2 Position vs. orientation perception

A novel feature of my line-matching task was the use of a probe line to represent the finger's orientation. Given that the nature of the display has an impact on responses, it would be interesting to examine how participants report finger orientation estimation using a line versus a single point in space. This comparison would clarify whether the findings I outlined above might be reasonably generalized to finger endpoint localization paradigms used by other researchers (e.g., [147]). Adding additional degrees of freedom to the probe adjustment (e.g., translation as well as rotation) would further help orient my suite of studies in the broader context of finger and hand perception.

Would we expect different response strategies for finger endpoint perception versus finger angle perception? Some evidence suggests a non-dominant limb advantage for matching limb position to a remembered joint angle, and a dominant limb advantage for matching the limb to endpoint location [56, 58, 60]. It has been argued that these data reflect a specialization of the nondominant and dominant limbs for force and position control, respectively [56, 58, 60, 151, 152]. If this is indeed the case, then it also implies that we use different strategies for representing endpoint locations versus intermediate orientations of the limbs. I did not find consistent evidence of a hand advantage in my orientation task, but comparing performance across a broader range of test probes could shed light on whether a hand advantage might exist for other strategies of hand and finger perception.

8.7.3 Perceived finger orientation and athleticism, musical ability and gaming experience

There is some evidence to suggest dancers have extremely accurate proprioceptive localization abilities [75, 146]. Other forms of physical training, or experience of working with the hands while not looking at them (for example, while playing an instrument or using video game controllers), might also lead to an improvement in localization ability over time. Repeatedly inferring, then confirming the position of the limbs with some manner of feedback, might lead to improved limb position and orientation sense over time. There are two ways to explore this possibility: first, I could compare performance in the line-matching task between individuals with dance or musical training, or who play video games regularly, with a control group. If I observed better accuracy in the trained individuals, I could then design a follow up experiment exploring finger orientation perception before and after some kind of training intervention, such as a dance class. Results from these studies would help us understand the time course of how proprioceptive position sense is calibrated and refined.

8.7.4 The effect of motivation on perceived finger orientation

In Chapter 5, I proposed that the addition of an experimenter seated in the testing room during the experiment may have inadvertently altered how participants approached the task. Specifically, I suggested that having an observer might prompt participants to shift to a more conservative strategy when adjusting the line to match their finger orientation. Currently, this is the most compelling explanation for the reversal in the direction of the rotational bias I observed in left index finger orientation perception, between experiments in Chapters 3 and 4 versus Chapter 5. Of course, this explanation requires additional experimental evidence to support it. In particular, it would be interesting to compare performance of participants in a block where an observer was present, versus a block where the experimenter was absent. If performance differed across blocks it would be a strong indicator that the observer's presence altered response strategies in the task. This result would be critically informative for the design of other studies on limb and body perception.

8.8 Conclusion

To build a comprehensive model of hand and finger perception, it is important to consider how the orientation of the fingers is perceived. In this dissertation I found a number of afferent contributions to finger orientation sense, including vestibular disruption, handedness, hand posture and muscle fatigue. I also demonstrated that characteristics of the test paradigm can have a large impact on participants' responses, which serves as a cautionary note for future experimental design and data interpretation. My findings suggest finger orientation sense is highly context-dependent and modulated by a number of bottom-up and top-down factors. I did not find compelling evidence for an internal body map with specific position characteristics that consistently biases finger orientation in predictable ways. This research has raised many additional questions which must be answered before a model of finger and hand position sense can be constructed with any degree of confidence. In particular, questions about drift of proprioceptive estimates over time, effects of muscle conditioning and fatigue, generalizability across perceptual tasks, individual differences in participants' training in limb and digit localization, and response strategies must be addressed. Nevertheless, my results contribute to a growing body of literature highlighting the complexity of finger, hand and limb localization. With more targeted behavioural and neuroimaging research, I am optimistic that we will arrive at a thorough understanding of how we perceive our limbs in space. This understanding may then form the basis for rehabilitation and training of limb perception and control, as well as the creation of intuitive artificial limbs.

Bibliography

[1] D. E. Adamo and B. J. Martin. Position sense asymmetry. *Experimental Brain Research*, 192(1):87–95, 2009.

[2] T. J. Allen, G. E. Ansems, and U. Proske. Effects of muscle conditioning on position sense at the human forearm during loading or fatigue of elbow flexors and the role of the sense of effort. *The Journal of physiology*, 580(2):423–434, 2007.

[3] J. M. Andre, N. Martinet, J. Paysant, J. M. Beis, and L. Le Chapelain. Temporary phantom limbs evoked by vestibular caloric stimulation in amputees. *Cognitive and Behavioral Neurology*, 14(3):190–196, 2001.

[4] E. Azañón and S. Soto-Faraco. Changing reference frames during the encoding of tactile events. *Current biology*, 18(14):1044–1049, 2008.

[5] E. Azañón, M.-P. Stenner, F. Cardini, and P. Haggard. Dynamic tuning of tactile localization to body posture. *Current Biology*, 25(4):512–517, 2015.

[6] M. Barnett-Cowan, R. T. Dyde, S. H. Fox, E. Moro, W. D. Hutchison, and L. R. Harris. Multisensory determinants of orientation perception in Parkinson's disease. *Neuroscience*, 167(4):1138–50, 2010.

[7] J. Begum Ali, D. Cowie, and A. J. Bremner. Effects of posture on tactile localization by 4 years of age are modulated by sight of the hands: Evidence for an early acquired external spatial frame of reference for touch. *Developmental Science*, 17(6):935–943, 2014.

[8] Y. Benjamini and Y. Hochberg. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B*

(Methodological), 57(1):289–300, 1995.

[9] P. Berens. CircStat: A MATLAB Toolbox for Circular Statistics. *Journal of Statistical Software*, 31(10):1–21, 2009.

[10] F. Binkofski, K. Reetz, and A. Blangero. Tactile agnosia and tactile apraxia: Cross talk between the action and perception streams in the anterior intraparietal area. *Behavioral and Brain Sciences*, 30(2):201–202, 2007.

[11] N. Bolognini and A. Maravita. Proprioceptive alignment of visual and somatosensory maps in the posterior parietal cortex. *Current Biology*, 17(21):1890–1895, 2007.

[12] M. Botvinick and J. Cohen. Rubber hands 'feel' touch that eyes see. *Nature*, 391(6669):756, 1998.

[13] J. P. Bresciani, J. Blouin, K. Popov, C. Bourdin, F. Sarlegna, J. L. Vercher, and G. M. Gauthier. Galvanic vestibular stimulation in humans produces online arm movement deviations when reaching towards memorized visual targets. *Neuroscience Letters*, 318(1):34–38, 2002.

[14] P. Bromage and R. Melzack. Phantom limbs and the body schema. *Canadian Anaesthetist's Society Journal*, 21(3):267–274, 1974.

[15] L. E. Brown, D. a. Rosenbaum, and R. L. Sainburg. Limb position drift: implications for control of posture and movement. *Journal of Neurophysiology*, 90(5):3105–3118, 2003.

[16] L. J. Buxbaum and H. Branch Coslett. Specialised structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology*, 18(4):289–306, 2001.

[17] M. L. Cadieux, K. Whitworth, and D. I. Shore. Rubber hands do not cross the midline. *Neuroscience Letters*, 504(3):191–194, 2011.

[18] F. Clark, R. Burgess, J. W. Chapin, and W. Lipscomb. Role of intramuscular receptors in the awareness of limb position. *Journal of Neurophysiology*, 54(6):1529–1540, 1985.

[19] F. Clark, K. Horch, S. Bach, and G. Larson. Contributions of cutaneous and joint recep-

tors to static knee-position sense in man. *Journal of Neurophysiology*, 42(3):877–888, 1979.

[20] I. A. H. Clemens, M. De Vrijer, L. P. J. Selen, J. A. M. Van Gisbergen, and W. P. Medendorp. Multisensory processing in spatial orientation: an inverse probabilistic approach. *The Journal of Neuroscience*, 31(14):5365–5377, 2011.

[21] D. M. Clower, J. M. Hoffman, J. R. Votaw, T. L. Faber, R. P. Woods, and G. E. Alexander. Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature*, 383(6601):618, 1996.

[22] M. S. Cohen. Handedness questionnaire, 08 2009.

[23] D. F. Collins and A. Prochazka. Movement illusions evoked by ensemble cutaneous input from the dorsum of the human hand. *The Journal of Physiology (Lond.)*, 496(3):857–871, 1996.

[24] D. F. Collins, K. M. Refshauge, and S. C. Gandevia. Sensory integration in the perception of movements at the human metacarpophalangeal joint. *The Journal of Physiology (Lond.)*, 529(2):505–515, 2000.

[25] D. F. Collins, K. M. Refshauge, G. Todd, and S. C. Gandevia. Cutaneous receptors contribute to kinesthesia at the index finger, elbow, and knee. *Journal of Neurophysiology*, 94(3):1699–1706, 2005.

[26] B. Craske. Perception of impossible limb positions induced by tendon vibration. *Science*, 196(4285):71–73, 1977.

[27] E. K. Cressman and D. Y. P. Henriques. Sensory recalibration of hand position following visuomotor adaptation. *Journal of Neurophysiology*, 102(6):3505–3518, 2009.

[28] F. De Vignemont. Body schema and body image—pros and cons. *Neuropsychologia*, 48(3):669–680, 2010.

[29] F. De Vignemont, A. Majid, C. Jola, and P. Haggard. Segmenting the body into parts: evidence from biases in tactile perception. *The Quarterly Journal of Experimental Psychology*, 62(3):500–512, 2009.

[30] A. Di Vita, M. Boccia, L. Palermo, and C. Guariglia. To move or not to move, that is the question! body schema and non-action oriented body representations: An fmri meta-analytic study. *Neuroscience & Biobehavioral Reviews*, 68:37–46, 2016.

[31] H. C. Dijkerman and E. H. De Haan. Somatosensory processing subserving perception and action: Dissociations, interactions, and integration. *Behavioral and Brain Sciences*, 30(2):224–230, 2007.

[32] V. Dilda, H. G. MacDougall, I. S. Curthoys, and S. T. Moore. Effects of Galvanic vestibular stimulation on cognitive function. *Experimental Brain Research*, 216(2):275–285, 2012.

[33] J. Dlugaiczyk, K. D. Gensberger, and H. Straka. Galvanic vestibular stimulation: from basic concepts to clinical applications. *Journal of Neurophysiology*, 121(6):2237–2255, 2019.

[34] R. T. Dyde, M. R. Jenkin, and L. R. Harris. The subjective visual vertical and the perceptual upright. *Experimental Brain Research*, 173(4):612–622, 2006.

[35] B. B. Edin and N. Johansson. Skin strain patterns provide kinaesthetic information to the human central nervous system. *The Journal of Physiology (Lond.)*, 487:243–51, 1995.

[36] T. Elbert, C. Pantev, C. Wienbruch, B. Rockstroh, and E. Taub. Increased cortical representation of the fingers of the left hand in string players. *Science*, 270(5234):305–307, 1995.

[37] M. O. Ernst. *Optimal multisensory integration: Assumptions and limits*, chapter 30, pages 527–544. MIT Press, Cambridge, 2012.

[38] M. O. Ernst and M. S. Banks. Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, 415(6870):429–433, 2002.

[39] M. O. Ernst and H. H. Bülthoff. Merging the senses into a robust percept. *Trends in Cognitive Sciences*, 8(4):162–169, 2004.

[40] E. R. Ferrè, G. Bottini, and P. Haggard. Vestibular modulation of somatosensory per-

ception. *European Journal of Neuroscience*, 34(July):1337–1344, 2011.

[41] E. R. Ferrè, E. Vagnoni, and P. Haggard. Vestibular contributions to bodily awareness. *Neuropsychologia*, 51(8):1445–1452, 2013.

[42] W. R. Ferrell and A. Smith. The effect of digital nerve block on position sense at the proximal interphalangeal joint of the human index finger. *Brain research*, 425(2):369–371, 1987.

[43] W. R. Ferrell and A. Smith. Position sense at the proximal interphalangeal joint of the human index finger. *The Journal of Physiology (Lond.)*, 399(1):49–61, 1988.

[44] L. E. Fraser. Do the subjective visual vertical and the subjective haptic vertical probe a common estimate of gravitational upright? Master's thesis, York University, 2014.

[45] L. E. Fraser and L. R. Harris. Perceived finger orientation is biased towards functional task spaces. *Experimental Brain Research*, 234(12):3565–3574, 2016.

[46] L. E. Fraser and L. R. Harris. The effect of hand position on perceived finger orientation in left- and right-handers. *Experimental Brain Research*, 235(12):1–11, 2017.

[47] C. D. Frith, S.-J. Blakemore, and D. M. Wolpert. Abnormalities in the awareness and control of action. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 355(1404):1771–1788, 2000.

[48] S. C. Gandevia. Illusory movements produced by electrical stimulation of low-threshold muscle afferents from the hand. *Brain*, 108(4):965–981, 1985.

[49] S. C. Gandevia, J. L. Smith, M. Crawford, U. Proske, and J. L. Taylor. Motor commands contribute to human position sense. *The Journal of Physiology (Lond.)*, 571(Pt 3):703–710, 2006.

[50] M. Gentilucci, E. Daprati, and M. Gangitano. Right-handers and left-handers have different representations of their own hand. *Cognitive Brain Research*, 6(3):185–192, 1998.

[51] G. A. Gescheider. *Psychophysics: the fundamentals*. Psychology Press, 2013.

[52] M. F. Ghilardi, J. Gordon, and C. Ghez. Learning a visuomotor transformation in a local area of work space produces directional biases in other areas. *Journal of Neurophysiology*, 73(6):2535–2539, 1995.

[53] M. J. Giummarra, S. J. Gibson, N. Georgiou-Karistianis, and J. L. Bradshaw. Mechanisms underlying embodiment, disembodiment and loss of embodiment. *Neuroscience and Biobehavioral Reviews*, 32:143–160, 2008.

[54] M. J. Giummarra, S. J. Gibson, N. Georgiou-Karistianis, and J. L. Bradshaw. Mechanisms underlying embodiment, disembodiment and loss of embodiment. *Neuroscience and Biobehavioral Reviews*, 32:143–160, 2008.

[55] D. J. Goble and S. H. Brown. Task-dependent asymmetries in the utilization of proprioceptive feedback for goal-directed movement. *Experimental Brain Research*, 180(4):693–704, 2007.

[56] D. J. Goble and S. H. Brown. The biological and behavioral basis of upper limb asymmetries in sensorimotor performance. *Neuroscience and Biobehavioral Reviews*, 32(3):598–610, 2008.

[57] D. J. Goble and S. H. Brown. Upper limb asymmetries in the matching of proprioceptive versus visual targets. *Journal of Neurophysiology*, 99(6):3063–3074, 2008.

[58] D. J. Goble and S. H. Brown. Upper limb asymmetries in the perception of proprioceptively determined dynamic position sense. *Journal of Experimental Psychology: Human Perception and Performance*, 36(3):768–75, 2010.

[59] D. J. Goble, J. P. Coxon, N. Wenderoth, A. Van Impe, and S. P. Swinnen. Proprioceptive sensibility in the elderly: degeneration, functional consequences and plastic-adaptive processes. *Neuroscience & Biobehavioral Reviews*, 33(3):271–278, 2009.

[60] D. J. Goble, B. C. Noble, and S. H. Brown. Proprioceptive target matching asymmetries in left-handed individuals. *Experimental Brain Research*, 197(4):403–408, 2009.

[61] M. A. Goodale and A. D. Milner. Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1):20–25, 1992.

[62] M. S. Graziano. Where is my arm? the relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National Academy of Sciences*, 96(18):10418–10421, 1999.

[63] J. Gregory, D. Morgan, and U. Proske. Aftereffects in the responses of cat muscle spindles. *Journal of Neurophysiology*, 56(2):451–461, 1986.

[64] J. Gregory, D. Morgan, and U. Proske. Aftereffects in the responses of cat muscle spindles and errors of limb position sense in man. *Journal of Neurophysiology*, 59(4):1220–1230, 1988.

[65] M. Guerraz, J. Blouin, and J.-L. Vercher. From head orientation to hand control: evidence of both neck and vestibular involvement in hand drawing. *Experimental Brain Research*, 150:40–49, 2003.

[66] S. Hach and S. Schütz-Bosbach. Sinistrals' upper hand: Evidence for handedness differences in the representation of body space. *Brain and Cognition*, 72(3):408–418, 2010.

[67] P. Haggard, C. Newman, J. Blundell, and H. Andrew. The perceived position of the hand in space. *Perception & Psychophysics*, 62(2):363–377, 2000.

[68] J. Han, G. Waddington, R. Adams, J. Anson, and Y. Liu. Assessing proprioception: a critical review of methods. *Journal of Sport and Health Science*, 5(1):80–90, 2016.

[69] L. R. Harris, M. J. Carnevale, S. D'Amour, L. E. Fraser, V. Harrar, A. E. Hoover, C. Mander, and L. M. Pritchett. How our body influences our perception of the world. *Frontiers in Psychology*, 6:819, 2015.

[70] L. R. Harris, K. Sakurai, and W. H. Beaudot. Tactile flow overrides other cues to self motion. *Scientific Reports*, 7(1):1059, 2017.

[71] H. Head and G. Holmes. Sensory disturbances from cerebral lesions. *Brain*, 34(2-3):102–254, 1911.

[72] H. Holle, N. McLatchie, S. Maurer, and J. Ward. Proprioceptive drift without illusions of ownership for rotated hands in the "rubber hand illusion" paradigm. *Cognitive Neuro-*

science, 2(3-4):171–178, 2011.

[73] A. E. N. Hoover and L. R. Harris. The role of the viewpoint on body ownership. *Experimental Brain Research*, 233(4):1053–1060, 2015.

[74] M. Jeannerod. *The neural and behavioural organization of goal-directed movements.* Clarendon Press/Oxford University Press, New York, NY, US, 1988.

[75] C. Jola, A. Davis, and P. Haggard. Proprioceptive integration and body representation: insights into dancers' expertise. *Experimental Brain Research*, 213(2-3):257–265, 2011.

[76] M. Kammers, I. Van der Ham, and H. Dijkerman. Dissociating body representations in healthy individuals: differential effects of a kinaesthetic illusion on perception and action. *Neuropsychologia*, 44(12):2430–2436, 2006.

[77] M. P. Kammers, J. Mulder, F. de Vignemont, and H. C. Dijkerman. The weight of representing the body: addressing the potentially indefinite number of body representations in healthy individuals. *Experimental Brain Research*, 204(3):333–342, 2010.

[78] A. M. Kappers. The contributions of egocentric and allocentric reference frames in haptic spatial tasks. *Acta Psychologica*, 117(3):333–340, 2004.

[79] A. M. Kappers, A. Postma, and R. F. Viergever. How robust are the deviations in haptic parallelity? *Acta Psychologica*, 128(1):15–24, 2008.

[80] A. M. L. Kappers. Large systematic deviations in the haptic perception of parallelity. *Perception*, 28(8):1001–1012, 1999.

[81] A. M. L. Kappers and J. J. Koenderink. Haptic perception of spatial relations. *Perception*, 28(6):781–795, 1999.

[82] A. M. L. Kappers and R. F. Viergever. Hand orientation is insufficiently compensated for in haptic spatial perception. *Experimental Brain Research*, 173:407–414, 2006.

[83] J. Keller and D. Sekaquaptewa. Solo status and women's spatial test performance: the role of individuation tendencies. *European Journal of Social Psychology*, 38(6):1044–

1053, 2008.

[84] A. Z. Khan, L. Pisella, and G. Blohm. Causal evidence for posterior parietal cortex involvement in visual-to-motor transformations of reach targets. *Cortex*, 49(9):2439–2448, 2013.

[85] K. Kilteni, J. M. Normand, M. V. Sanchez-Vives, and M. Slater. Extending body space in immersive virtual reality: A very long arm illusion. *PLoS ONE*, 7(7), 2012.

[86] S.-G. Kim, J. Ashe, K. Hendrich, J. M. Ellermann, H. Merkle, K. Ugurbil, and A. P. Georgopoulos. Functional magnetic resonance imaging of motor cortex: hemispheric asymmetry and handedness. *Science*, 261(5121):615–617, 1993.

[87] J. King, E. Harding, and A. Karduna. The shoulder and elbow joints and right and left sides demonstrate similar joint position sense. *Journal of Motor Behavior*, 45(6):479–486, 2013.

[88] J. J. Knox, M. W. Coppieters, and P. W. Hodges. Do you know where your arm is if you think your head has moved? *Experimental Brain Research*, 173:94–101, 2006.

[89] A. Kwan, P. A. Forbes, D. E. Mitchell, J.-S. Blouin, and K. E. Cullen. Neural substrates, dynamics and thresholds of galvanic vestibular stimulation in the behaving primate. *Nature Communications*, 10(1):1904, 2019.

[90] J. R. Lackner. Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain*, 111(2):281–297, 1988.

[91] J. R. Lackner and P. DiZio. Vestibular, proprioceptive, and haptic contributions to spatial orientation. *Annual Review of Psychology*, 56:115–147, 2005.

[92] B. Lenggenhager, C. Lopez, and O. Blanke. Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations. *Experimental Brain Research*, 184(2):211–221, 2008.

[93] J.-C. Lepecq, C. De Waele, S. Mertz-Josse, C. Teyssèdre, P. T. B. Huy, P.-M. Baudonnière, and P.-P. Vidal. Galvanic vestibular stimulation modifies vection paths in healthy subjects. *Journal of Neurophysiology*, 95:3199–3207, 2006.

[94] R. L. Lieber, M. D. Jacobson, B. M. Fazeli, R. A. Abrams, and M. J. Botte. Architecture of selected muscles of the arm and forearm: anatomy and implications for tendon transfer. *The Journal of Hand Surgery*, 17(5):787–798, 1992.

[95] S. A. Linkenauger, M. N. Geuss, J. K. Stefanucci, M. Leyrer, B. H. Richardson, D. R. Proffitt, H. H. Bülthoff, and B. J. Mohler. Evidence for hand-size constancy: the dominant hand as a natural perceptual metric. *Psychological Science*, 25(11):2086–2094, 2014.

[96] S. A. Linkenauger, M. Leyrer, H. H. Bülthoff, and B. J. Mohler. Welcome to wonderland: The influence of the size and shape of a virtual hand on the perceived size and shape of virtual objects. *PloS ONE*, 8(7):e68594, 2013.

[97] S. A. Linkenauger, J. K. Witt, J. Z. Bakdash, J. K. Stefanucci, and D. R. Proffitt. Asymmetrical body perception: A possible role for neural body representations. *Psychological Science*, 20(11):1373–1380, 2009.

[98] S. G. Lomber and S. Malhotra. Double dissociation of 'what' and 'where' processing in auditory cortex. *Nature Neuroscience*, 11(5):609, 2008.

[99] M. R. Longo. The effects of immediate vision on implicit hand maps. *Experimental Brain Research*, 232(4):1241–1247, Apr 2014.

[100] M. R. Longo. Posture modulates implicit hand maps. *Consciousness and Cognition*, 36:96–102, 2015.

[101] M. R. Longo. Distorted body representations in healthy cognition. *The Quarterly Journal of Experimental Psychology*, 70(3):378–388, 2017.

[102] M. R. Longo, E. Azañón, and P. Haggard. More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia*, 48(3):655–668, 2010.

[103] M. R. Longo and P. Haggard. An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences of the United States of America*, 107(26):11727–11732, 2010.

[104] M. R. Longo and P. Haggard. A 2.5-D representation of the human hand. *Journal of*

Experimental Psychology: Human Perception and Performance, 38(1):9–13, 2012.

[105] M. R. Longo and P. Haggard. Implicit body representations and the conscious body image. *Acta Psychologica*, 141(2):164–168, 2012.

[106] M. R. Longo and R. Morcom. No Correlation between Distorted Body Representations Underlying Tactile Distance Perception and Position Sense. *Frontiers in Human Neuroscience*, 10(November):1–8, 2016.

[107] C. Lopez. Making Sense of the Body: the Role of Vestibular Signals. *Multisensory Research*, 28:525–557, 2015.

[108] C. Lopez, B. Lenggenhager, and O. Blanke. How vestibular stimulation interacts with illusory hand ownership. *Consciousness and Cognition*, 19(1):33–47, 2010.

[109] C. Lopez, H.-M. M. Schreyer, N. Preuss, and F. W. Mast. Vestibular stimulation modifies the body schema. *Neuropsychologia*, 50(8):1830–1837, 2012.

[110] J. L. Lugrin, J. Latt, and M. E. Latoschik. Avatar anthropomorphism and illusion of body ownership in VR. *2015 IEEE Virtual Reality Conference, VR 2015 - Proceedings*, pages 229–230, 2015.

[111] H. G. MacDougall, A. E. Brizuela, A. M. Burgess, and I. S. Curthoys. Between-subject variability and within-subject reliability of the human eye-movement response to bilateral galvanic (DC) vestibular stimulation. *Experimental Brain Research*, 144(1):69–78, 2002.

[112] H. G. MacDougall, S. T. Moore, I. S. Curthoys, and F. O. Black. Modeling postural instability with Galvanic vestibular stimulation. *Experimental Brain Research*, 172(2):208–220, 2006.

[113] F. Mancini, M. R. Longo, G. D. Iannetti, and P. Haggard. A supramodal representation of the body surface. *Neuropsychologia*, 49(5):1194–1201, 2011.

[114] Z.-H. Mao, H.-N. Lee, R. J. Sclabassi, and M. Sun. Information capacity of the thumb and the index finger in communication. *IEEE Transactions on Biomedical Engineering*, 56(5):1535–1545, 2009.

[115] F. Mars, P. S. Archambault, and A. G. Feldman. Vestibular contribution to combined arm and trunk motion. *Experimental Brain Research*, 150(4):515–519, 2003.

[116] M. Martel, L. Cardinali, A. C. Roy, and A. Farnè. Tool-use: An open window into body representation and its plasticity. *Cognitive Neuropsychology*, 33:1–20, 2016.

[117] F. W. Mast. Does the world rock when the eyes roll? Allocentric orientation representation, ocular counterroll, and the subjective visual vertical. *Swiss Journal of Psychology*, 59(2):89, 2000.

[118] F. W. Mast, D. M. Merfeld, and S. M. Kosslyn. Visual mental imagery during caloric vestibular stimulation. *Neuropsychologia*, 44(1):101–109, 2006.

[119] P. Matthews. Muscle spindles and their motor control. *Physiological Reviews*, 44(2):219–288, 1964.

[120] P. B. Matthews. Proprioceptors and their contribution to somatosensory mapping; complex messages require complex processing. *Canadian Journal of Physiology and Pharmacology*, 66(4):430–438, 1988.

[121] S. Mattioni and M. R. Longo. The effects of verbal cueing on implicit hand maps. *Acta Psychologica*, 153:60–65, 2014.

[122] M. S. McGlone and J. Aronson. Stereotype threat, identity salience, and spatial reasoning. *Journal of Applied Developmental Psychology*, 27(5):486–493, 2006.

[123] J. Medina and H. B. Coslett. From maps to form to space: Touch and the body schema. *Neuropsychologia*, 48(3):645–654, 2010.

[124] J. Medina, S. A. Jax, M. J. Brown, and H. B. Coslett. Contributions of efference copy to limb localization: Evidence from deafferentation. *Brain Research*, 1355:104–111, 2010.

[125] R. Melzack and P. Bromage. Experimental phantom limbs. *Experimental Neurology*, 39(2):261–269, 1973.

[126] L. E. Miller, M. R. Longo, and A. P. Saygin. Mental body representations retain homuncular shape distortions: Evidence from Weber's illusion. *Consciousness and Cog-*

nition, 40:17–25, 2016.

[127] H. Mittelstaedt. *The formation of the visual and the postural vertical*, pages 147–155. Springer, Boston, MA, 1995.

[128] H. Mittelstaedt. Somatic graviception. *Biological Psychology*, 42(1):53–74, 1996.

[129] S. T. Moore, H. G. MacDougall, B. T. Peters, J. J. Bloomberg, I. S. Curthoys, and H. S. Cohen. Modeling locomotor dysfunction following spaceflight with galvanic vestibular stimulation. *Experimental Brain Research*, 174(4):647–659, 2006.

[130] G. L. Moseley and P. Brugger. Interdependence of movement and anatomy persists when amputees learn a physiologically impossible movement of their phantom limb. *Proceedings of the National Academy of Sciences of the United States of America*, 106(44):18798–18802, 2009.

[131] G. L. Moseley, A. Gallace, and C. Spence. Bodily illusions in health and disease: Physiological and clinical perspectives and the concept of a cortical 'body matrix'. *Neuroscience and Biobehavioral Reviews*, 36:34–46, 2012.

[132] R. C. Oldfield. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1):97–113, 1971.

[133] J. Paillard. *Body Schema and body image-a double dissociation*, pages 197–214. Academic Publishing House, Sofia, Bulgaria, 1999.

[134] L. Palermo, A. Di Vita, L. Piccardi, M. Traballesi, and C. Guariglia. Bottom-up and top-down processes in body representation: A study of brain-damaged and amputee patients. *Neuropsychology*, 28(5):772, 2014.

[135] F. Pavani, C. Spence, and J. Driver. Visual capture of touch: Out-of-the-body experiences with rubber gloves. *Psychological Science*, 11(5):353–359, 2000.

[136] W. Penfield and E. Boldrey. Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, 60, 1937.

[137] V. Pettorossi, R. Panichi, F. Botti, A. Kyriakareli, A. Ferraresi, M. Faralli, M. Schieppati,

and A. Bronstein. Prolonged asymmetric vestibular stimulation induces opposite, long-term effects on self-motion perception and ocular responses. *The Journal of Physiology*, 591(7):1907–1920, 2013.

[138] L. M. Pritchett and L. R. Harris. Perceived touch location is coded using a gaze signal. *Experimental Brain Research*, 213(2-3):229–234, 2011.

[139] U. Proske. What is the role of muscle receptors in proprioception? *Muscle & Nerve*, 31(6):780–787, 2005.

[140] U. Proske and S. C. Gandevia. The kinaesthetic senses. *The Journal of Physiology*, 587(Pt 17):4139–4146, 2009.

[141] U. Proske and S. C. Gandevia. The proprioceptive senses: their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, 92(4):1651–1697, 2012.

[142] U. Proske, D. L. Morgan, and J. E. Gregory. Thixotropy in skeletal muscle and in muscle spindles: a review. *Progress in Neurobiology*, 41(6):705–721, 1993.

[143] A. Przybyla, D. C. Good, and R. L. Sainburg. Dynamic dominance varies with handedness: Reduced interlimb asymmetries in left-handers. *Experimental Brain Research*, 216(3):419–431, 2012.

[144] H. G. Qureshi, A. A. Butler, G. K. Kerr, S. C. Gandevia, and M. E. Héroux. The hidden hand is perceived closer to midline. *Experimental Brain Research*, pages 1–7, 2019.

[145] V. S. Ramachandran and W. Hirstein. The perception of phantom limbs. the do hebb lecture. *Brain*, 121(9):1603–1630, 1998.

[146] J. R. E. Ramsay and M. J. Riddoch. Position-matching in the upper limb: professional ballet dancers perform with outstanding accuracy. *Clinical Rehabilitation*, 15(3):324–330, 2001.

[147] L. Rincon-Gonzalez, C. A. Buneo, and S. I. Tillery. The proprioceptive map of the arm is systematic and stable, but idiosyncratic. *PLoS ONE*, 6(11):25214, 2011.

[148] G. Rode, N. Charles, M.-T. Perenin, A. Vighetto, M. Trillet, and G. Aimard. Partial remission of hemiplegia and somatoparaphrenia through vestibular stimulation in a case of unilateral neglect. *Cortex*, 28(2):203–208, 1992.

[149] M. Rohde, M. Luca, and M. O. Ernst. The rubber hand illusion: Feeling of ownership and proprioceptive drift Do not go hand in hand. *PLoS ONE*, 6(6), 2011.

[150] W. Rymer and A. d'Almeida. Joint position sense: the effects of muscle contraction. *Brain*, 103(1):1–22, 1980.

[151] R. L. Sainburg. Evidence for a dynamic-dominance hypothesis of handedness. *Experimental Brain Research*, 142(2):241–258, 2002.

[152] R. L. Sainburg. Handedness: differential specializations for control of trajectory and position. *Exercise and Sport Sciences Reviews*, 33(4):206–213, 2005.

[153] A. F. Sanders and A. M. Kappers. Haptically straight lines. *Perception*, 36(11):1682–1697, 2007.

[154] F. E. Satterthwaite. An approximate distribution of estimates of variance components. *Biometrics bulletin*, 2(6):110–114, 1946.

[155] T. Schicke and B. Röder. Spatial remapping of touch: confusion of perceived stimulus order across hand and foot. *Proceedings of the National Academy of Sciences*, 103(31):11808–11813, 2006.

[156] L. Schmidt, F. Artinger, O. Stumpf, and G. Kerkhoff. Differential effects of galvanic vestibular stimulation on arm position sense in right- vs. left-handers. *Neuropsychologia*, 51(5):893–899, 2013.

[157] L. Schmidt, L. Depper, and G. Kerkhoff. Effects of age, sex and arm on the precision of arm position sense-left-arm superiority in healthy right-handers. *Frontiers in Human Neuroscience*, 7:915, 2013.

[158] L. Schmidt, I. Keller, K. S. Utz, F. Artinger, O. Stumpf, and G. Kerkhoff. Galvanic Vestibular Stimulation Improves Arm Position Sense in Spatial Neglect: A Sham-Stimulation-Controlled Study. *Neurorehabilitation and Neural Repair*, 27:497–506,

2013.

[159] R. J. Schwarz and C. Taylor. The anatomy and mechanics of the human hand. *Artificial limbs*, 2(2):22–35, 1955.

[160] J. Schwoebel and H. B. Coslett. Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience*, 17(4):543–553, 2005.

[161] D. I. Shore, E. Spry, and C. Spence. Confusing the mind by crossing the hands. *Cognitive Brain Research*, 14(1):153–163, 2002.

[162] A. Sirigu, J. Grafman, K. Bressler, and T. Sunderland. Multiple representations contribute to body knowledge processing: Evidence from a case of autotopagnosia. *Brain*, 114(1):629–642, 1991.

[163] J. L. Smith, M. Crawford, U. Proske, J. L. Taylor, and S. C. Gandevia. Signals of motor command bias joint position sense in the presence of feedback from proprioceptors. *Journal of Applied Physiology*, 106(3):950–958, 2009.

[164] P. Sörös, S. Knecht, T. Imai, S. Gürtler, B. Lütkenhöner, E. B. Ringelstein, and H. Henningsen. Cortical asymmetries of the human somatosensory hand representation in right-and left-handers. *Neuroscience Letters*, 271(2):89–92, 1999.

[165] D. N. Suprak, L. R. Osternig, P. van Donkelaar, and A. R. Karduna. Shoulder joint position sense improves with external load. *Journal of Motor Behavior*, 39(6):517–525, 2007.

[166] M. Tsakiris. My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*, 48:703–712, 2010.

[167] M. Tsakiris, L. Carpenter, D. James, and A. Fotopoulou. Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research*, 204(3):343–352, 2010.

[168] M. Tsakiris, M. Costantini, and P. Haggard. The role of the right temporo-parietal junction in maintaining a coherent sense of one's body. *Neuropsychologia*, 46:3014–3018, 2008.

[169] M. Tsakiris and P. Haggard. The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance*, 31(1):80, 2005.

[170] A. Tsay, T. J. Allen, and U. Proske. Position sense at the human elbow joint measured by arm matching or pointing. *Experimental Brain Research*, 234(10):2787–2798, 2016.

[171] G. Vallar and R. Ronchi. Somatoparaphrenia: A body delusion. A review of the neuropsychological literature. *Experimental Brain Research*, 192(3):533–551, 2009.

[172] R. J. Van Beers, A. C. Sittig, J. J. D. van der Gon, and J. J. Denier Van Der Gon. The precision of proprioceptive position sense. *Experimental Brain Research*, 122(4):367–377, 1998.

[173] G. Vingerhoets, F. Acke, A. S. Alderweireldt, J. Nys, P. Vandemaele, and E. Achten. Cerebral lateralization of praxis in right- and left-handedness: Same pattern, different strength. *Human Brain Mapping*, 33(4):763–777, 2012.

[174] R. Volcic and A. M. L. Kappers. Allocentric and egocentric reference frames in the processing of three-dimensional haptic space. *Experimental Brain Research*, 188(2):199–213, 2008.

[175] K. Volkening, J. Bergmann, I. Keller, M. Wuehr, F. Müller, and K. Jahn. Verticality perception during and after galvanic vestibular stimulation. *Neuroscience Letters*, 581:75–79, 2014.

[176] L. Walsh, C. Hesse, D. Morgan, and U. Proske. Human forearm position sense after fatigue of elbow flexor muscles. *The Journal of Physiology*, 558(2):705–715, 2004.

[177] J. P. Wann and S. F. Ibrahim. Does limb proprioception drift? *Experimental Brain Research*, 91(1):162–166, 1992.

[178] A. B. Watson and D. G. Pelli. QUEST: a Bayesian adaptive psychometric method. *Perception & Psychophysics*, 33(2):113–120, 1983.

[179] E. T. Wilson, J. Wong, and P. L. Gribble. Mapping proprioception across a 2D horizontal workspace. *PLoS ONE*, 5(7):e11851, 2010.

[180] J. Winter, T. Allen, and U. Proske. Muscle spindle signals combine with the sense of effort to indicate limb position. *The Journal of Physiology*, 568(3):1035–1046, 2005.

[181] S. Yamamoto and S. Kitazawa. Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience*, 4(7):759–765, 2001.

[182] K. Zilles, A. Schleicher, C. Langemann, K. Amunts, P. Morosan, N. Palomero-Gallagher, T. Schormann, H. Mohlberg, U. Bürgel, H. Steinmetz, et al. Quantitative analysis of sulci in the human cerebral cortex: development, regional heterogeneity, gender difference, asymmetry, intersubject variability and cortical architecture. *Human brain mapping*, 5(4):218–221, 1997.

[183] N. Zmyj, J. Jank, S. Schütz-Bosbach, and M. M. Daum. Detection of visual–tactile contingency in the first year after birth. *Cognition*, 120(1):82–89, 2011.

[184] S. Zuidhoek, A. M. L. Kappers, and A. Postma. Haptic orientation perception: Sex differences and lateralization of functions. *Neuropsychologia*, 45(2):332–341, 2007.

[185] S. Zuidhoek, A. M. L. Kappers, R. H. J. van der Lubbe, and A. Postma. Delay improves performance on a haptic spatial matching task. *Experimental Brain Research*, 149(3):320–30, 2003.